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Physiological and ecological determinants of nutrient partitioning in caribou and reindeer

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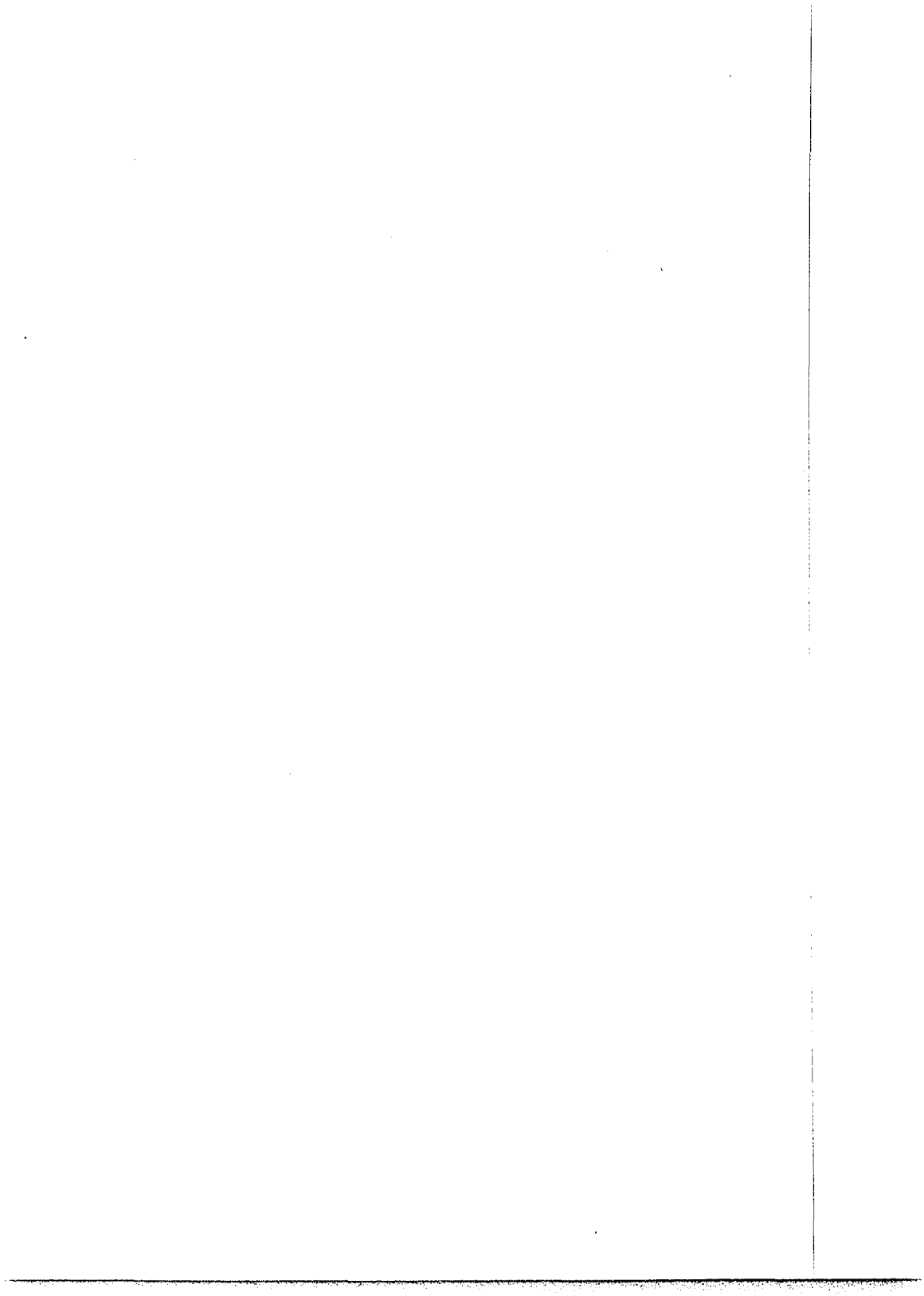

PHYSIOLOGICAL AND ECOLOGICAL DETERMINANTS OF NUTRIENT PARTITIONING IN CARIBOU AND REINDEER

A

THESIS

Presented to the Faculty of the University of Alaska Fairbanks

in Partial Fulfillment of the Requirements

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DOCTOR OF PHILOSOPHY

By

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PHYSIOLOGICAL AND ECOLOGICAL DETERMINANTS OF NUTRIENT PARTITIONING IN CARIBOU AND REINDEER

By

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Abstract

The effects of season, migration, and reproduction on the adipose and protein dynamics of barren-ground caribou were determined from field collections of adult females from the Porcupine Herd. Radio-collared females recaptured over time provided data on animals of known reproductive status. Pregnant females averaged a daily loss of 50g body fat and 15g body protein during the last 60 days of gestation. Between June and September, lactating females preferentially deposited body protein but non-lactating females preferentially deposited body fat. In both cohorts, fat deposition increased relative to protein deposition in fall, but maximum fat deposition occurred in summer. Females that conceived averaged 220% more body fat and 17% more body protein than females that did not conceive. Fetal and birth weight positively correlated with maternal protein reserves, but not with maternal fat reserves.

Fieldwork on free-ranging caribou were complemented with nutritional experiments on captive animals to determine the effects of energy intake, protein intake, the dietary protein:energy ratio, date, and body condition on nutrient partitioning between fat and protein deposition, and between maternal tissue deposition and milk production. In both lactating and non-lactating females, the proportion of tissue deposited as fat rather than protein increased between spring and fall but decreased with increasing fatness. Lactating and non-lactating females had comparable efficiency coefficients for net energy retention (60% and 65% respectively), but daily maintenance requirement for lactating females (456 $KJ/BW^{0.75}$) was twice that for non-lactating individuals (233 $KJ/BW^{0.75}$). Energy intake increased protein deposition in lactating females but increased fat deposition in non-lactating females. Production of milk dry

matter, fat, and energy were unaffected by maternal energy intake, maternal protein intake, maternal body condition, or calf age. However, production of milk lactose correlated with maternal energy intake, while production of milk protein correlated with the maternal dietary protein:energy ratio.

Prediction equations for body weight and composition of barren-ground caribou were developed using bone, muscle, fat, and organ indices. Prediction equations for body weight were validated with an independent data set.

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Whitten's good aim netted 68 female caribou and, through mistaken identity, 5 bulls. Mike Smith triumphed as Mikeintosh director, while Carol Nielsen offered both veterinary expertise as well as friendly encouragement. Terry Bowyer made sense of unintelligible printouts begging for statistical direction.

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Introduction

Caribou and reindeer (*Rangifer tarandus*) are one of only two ungulate species to have successfully colonized the arctic (Klein 1986). Their unequivocal success in northern latitudes is underscored by both a circumpolar distribution and a world population numbering 3.3 to 3.9 million animals (Williams and Heard 1986).

The success of caribou and reindeer in a harshly unforgiving environment testify to the adaptiveness of numerous traits that have evolved in response to seasonal extremes in photoperiod, temperature, and food resources. Many of these adaptive traits are directed towards nutrient acquisition and conservation, and include an insulative pelage that allows thermoneutrality to -40C (Nilssen et al. 1984, Timisjarvi et al. 1984), counter-current heat exchangers in the nasal cavity (Blix and Johnsen 1983) and legs (Irving and Krog 1955), and lateral metapodial digits that minimize foot loading (Thing 1977, Fancy and White 1985) and facilitate cratering in snow. Additionally, increased appetite drive in summer (McEwan and Whitehead 1970, Larsen et al. 1985) and selective grazing of plant species and plant communities collectively (Kuropat and Bryant 1980, Skogland 1980, White and Trudell 1980, White 1983, Martell and Russell unpub. data, Klein 1986) maximize nutrient intake during the brief growing season.

Beyond the acquisition and conservation of energy and nutrients, the partitioning of these energy and nutrients among competing body tissues adds another dimension to maximizing fitness. In caribou and reindeer, an adaptive partitioning strategy is especially critical given the vital role of body composition in virtually

every aspect of survival and reproduction. Research on reindeer has clearly established associations between body composition and pregnancy rate (Klein and White 1978, Reimers 1983), puberty (Skogland 1983, Reimers 1983a, Leader-Williams and Rosser 1983) fetal growth (Skogland 1984), birth weight (Skogland 1983, 1984, Rognmo et al. 1983, Eloranta and Nieminen 1986), birth date (Skogland 1983), calf growth (Lenvik et al 1988, Rognmo et al. 1983, Eloranta and Niemenen 1986) and calf survival (Haukioja and Salovaara 1978). Comparable data for caribou are largely unavailable (Davis et al. 1991) but increasing evidence support a causal relationship between body weight and pregnancy rate (Dauphiné 1976, Cameron et al. 1991).

In breeding females, nutrient partitioning must allocate limited resources not only between adipose tissue and lean muscle, but also between maternal body reserves and calf production. Investment in the immediate offspring must be adequate to assure current recruitment, but at the same time, must not overly compromise either maternal life expectancy or future reproductive potential.

Nutrient partitioning and body composition dynamics are therefore critical to the biology of caribou and reindeer, but knowledge of this subject remains poor. While recent work has contributed much to the understanding of seasonal body composition patterns (Adamczewski et al. 1987, Tyler 1987, Huot 1989), some of the data are conflicting and many knowledge gaps remain. Additionally, non-seasonal factors that are likely to affect nutrient partitioning have not been addressed.

The objective of this study was to examine the role of various physiological and ecological factors that may affect nutrient partitioning in adult female caribou and reindeer. In Chapter 1, I focus on ecological determinants of nutrient partitioning and

evaluate the effects of season, migration, and reproductive status on body weight and body composition of free-ranging female barren-ground caribou (*R. t. granti*) from the Porcupine Herd. I also examine how body weight and composition will in turn affect pregnancy rate, fetal growth, and birth weight. In Chapter 2, I use captive barren-ground caribou and reindeer (*R. t. tarandus*) to address the role of physiological determinants in nutrient partitioning. In this chapter, I evaluate the effects of protein and energy intake, the dietary protein:energy ratio, body condition, and season on nutrient partitioning in lactating and non-lactating females. In Chapter 3, I consider management applications that derive from knowledge of body composition dynamics. I document the deposition and mobilization patterns of various fat depots, and explore the ramifications of using fat indices to predict body condition. I develop prediction equations of body weight and composition for female barren-ground caribou using bone, muscle, organ, and fat indices that can be collected from hunter-killed animals in a population monitoring program.

Chapter 1.
Seasonal and Reproductive Effects on Body Composition and Breeding Potential of Barren-ground Caribou

Introduction

Northern ungulates undergo pronounced fluctuations in body reserves (Wood et al. 1962, Mitchell et al. 1976, Reimers et al. 1982, Adamczewski et al. 1987, Huot 1989) as an adaptation to their highly seasonal environments. During the brief summer when high quality forage is abundant, animals rapidly deposit body tissue to make up for large over-winter losses. Among free-ranging caribou and reindeer, summer weight gain in adult females averages 190 g/d and may reach 375 g/d (Reimers 1983a). In winter, weight attrition averages 60 g/d, with a maximal loss rate of 140 g/d reported for Svalbard reindeer (Reimers 1983a).

Although seasonal fluctuations in body reserves are well documented, the published literature on *Rangifer* debates the relative importance of summer versus winter nutrition in the expression of body size and composition (Reimers 1983a, Skogland 1983, Shideler et al. 1986), the importance of carry-over effects from one season to another, and even the direction and magnitude of seasonal composition changes. Despite general agreement that body reserves in female caribou reach an annual low shortly after calving (Dauphiné 1976, Adamczewski et al. 1987), reported changes in fat reserves between fall and mid-winter have been less consistent. Dauphiné (1976) and Adamczewski et al. (1987) both documented declines in fat indices during this period but did not separate the confounding effects of reproductive

expenditure. In contrast, Huot (1989), who determined total body fat content for both breeding and non-breeding caribou, did not find any depletion of fat reserves between fall and mid-April in any age-class. Additionally, he did not find any change in calf body weights during this interval. Among adult females, winter weight loss could be solely attributed to reductions in protein reserves (Huot 1989).

The published literature also debates the role of body reserves in the life-history strategy of *Rangifer*. Body reserves have been shown to affect both the probability of winter survival (Klein 1968, Thomas et al. 1976, Reimers et al. 1982) as well as the probability of reproductive success (Dauphiné 1976, Klein and White 1978, Haukioja and Salovaara 1978, Reimers 1983a, 1983b, Skogland 1983, 1984, Rognmo et al. 1983, White and Luick 1984, Lenvik et al. 1988, Cameron et al. 1991). However, Tyler (1987) dismisses the role of fat reserves for enhancing winter survival, arguing that adipose tissues must primarily serve a reproductive function because they can contribute to only 25% of winter energy requirements in female Svalbard reindeer (Tyler 1986). Other researchers (Davis et al. 1991) counter this argument for caribou, maintaining that the demonstrated link between pregnancy rate and body composition is limited to semi-domesticated reindeer which do not experience the same selective pressures for reproduction as wild caribou. They noted no significant change in mean body weight of barren-ground caribou from the Delta Herd despite a drop in the parturition rate from 67 to 0% in 24-month old females.

The objective of this study was to evaluate the effects of season and reproduction on body weight and body composition in adult female caribou from the Porcupine Herd, and to examine the effects of body composition on future reproductive potential. Null hypotheses being tested were:

Ho_1: Differential energy demands between breeding and non-breeding female caribou will lead to differential seasonal strategies in the deposition and mobilization of body reserves in these cohorts.

Ho_2: Pregnancy rate positively correlates to maternal body fat and protein reserves.

Ho_3: Fetal growth and birth weight positively correlate to maternal body fat and protein reserves.

Methods

The Porcupine Caribou Herd currently numbers 178,000 animals (Fancy et al. 1990) following a decade of steady population expansion (Garner and Reynolds 1986). The population is highly migratory, with an extensive distribution covering 250,000 km^2 (64-70°N, 130-150°W) in northeastern Alaska, northern Yukon Territory, and northwestern Northwest Territories. Calving occurs in early June on the arctic coastal tundra along the Beaufort Sea between Babbage River in the Yukon Territory, and Canning River in Alaska (Garner and Reynolds 1986, Eastland et al. 1989). In July and early August, the caribou form post-calving aggregations numbering tens of thousands of individuals, and travel extensively with movements of up to 26 km per day (Fancy et al. 1989) to seek relief from black flies, mosquitos, and bot and warble flies. Post-calving aggregations disperse by mid-August but animals continue to travel extensively in a non-directional manner. Fall migration occurs in late October (Eastland 1991) and coincides with the rut (Garner and Reynolds 1986). Winter distributions are primarily in the central Yukon Territory and in northeastern Alaska in the vicinity of Arctic Village. Spring migration begins in early March, with groups of pregnant females preceding barren females and bulls.

Reproductively-active and reproductively-inactive adult female caribou were collected four times annually in both 1987 and 1988, in March-April, June, September, and late November. A reproductively-active female is defined as being pregnant in March-April, calving in June, lactating in September, and weaning in November. Reproductively-inactive females, although sexually mature, either failed to conceive or failed to lactate because of calf loss. Reproductive status as defined pertains to only one breeding cycle and does not account for the presence or absence

of a fetus in November. Thus, both reproductively-active as well as reproductively-inactive females may have conceived during the October rut.

In both 1987 and 1988, June collections occurred on the calving grounds at Beaufort Lagoon, September collections occurred during the fall migration as animals crossed the Porcupine River near Old Crow, and November collections occurred on the winter ranges at Eagle Plains in the central Yukon Territory. The March-April collection also occurred at Eagle Plains in 1988 but took place near Arctic Village in 1987 after the population drifted west from the central Yukon.

In addition to these seasonal collections, a class of non-lactating females were experimentally created in June 1987 by removing the newborn calves from 10 females. These females were radio-collared and released, then relocated and sacrificed over the subsequent year to assess the effects of a lactational pause on body composition.

Reproductive status of harvested animals was determined by the presence or absence of a fetus in March and April, the presence of a neonate in June, and lactational status in September. In November, recent weaning in some females necessitated the dual criteria of both mammary fluid and a calf-at-foot as definitive evidence of lactation during the previous summer. Additionally, the uterus was carefully flushed for the presence of an unimplanted fetus which may have been conceived several weeks earlier during the rut. Gravid uteri in March-April were weighed and its nutritional contents calculated using fat (1.19%), protein (8.97%), and ash (1.87%) compositions reported by Huot (1989) for the fetus, uterus, and uterine fluids of caribou. Newborn calves in June were sexed and weighed.

Shot animals were immediately weighed, processed at field camps (Chapter 3), and then frozen at -15C until laboratory analysis. Carcasses were then

reweighed at that time and correction was made for water loss during storage. Chemical determination of fat, water, nitrogen and ash content were conducted in 2-4 replicate samples of carcass and visceral sawdust homogenates (Huot and Picard 1988). Homogenate samples were analysed for fat content using the methanol-chloroform technique (Christie 1982), and freeze-dried 72 hours for determination of water content. Kjeldahl analysis was conducted on samples already extracted for fat and water (i.e. fat-free dry matter), and resultant nitrogen values multiplied by 6.25 to give crude protein. Protein reserves are therefore reported on a dry-weight basis. Fat-free dry tissues were also combusted at 500C for 8 hours to give ash content.

Body weight in this study refers to animal weight immediately after shooting. Combined carcass and viscera (carcass+viscera) weight equals body weight minus the weights of skull, antlers, hide, and gastrointestinal content. Total body composition was derived from the weighted compositions of carcass and viscera, and therefore excludes composition of the skull, antlers, and hide. Aging was conducted by microscopic examination of cementum annuli in the first incisor (Matson's Laboratory, MT).

Body weight, carcass+viscera weight, protein composition, and ash composition were standardized for skeletal dimension after analysis of variance (ANOVA) revealed significant inter-sample differences in body length, hindfoot length, and metatarsus length. The two reproductive cohorts also differed significantly in length of femur in September 1987. Femur length was the only skeletal dimension significantly affecting either body weight or carcass+viscera weight. Consequently, body weight was standardized to the mean femur length of 28.3 cm, at a scaling factor of 5.6 kg/cm. Carcass+viscera weight was similarly downscaled at 3.06 kg/cm for femurs longer than the mean, and upscaled at the same

factor for femurs shorter than the mean. Both protein and ash composition were significantly affected by only metatarsus length. The arcsine transformed (Zar 1984) protein percentage was downscaled by a factor of 0.0102 units/cm for metatarsi longer than the mean of 30.5 cm, and upscaled by the same factor for metatarsi shorter than this mean. The arcsine transformed (Zar 1984) ash percentage was scaled accordingly at a factor of 0.0131 units/cm deviation from the mean. Body fat composition was not significantly affected by skeletal dimensions and therefore was not scaled.

Least squares ANOVA for unbalanced data (SAS Institute 1985) was used to evaluate significant differences between season and reproductive cohort. Duncan's studentized range test was used for multiple comparison of means. 1987 and 1988 data were pooled where the year and year-by-season effects were not significant. Significance was established at $p<0.05$.

Deposition and mobilization rates were computed for body fat and body protein by dividing interseasonal differences by the number of days between collections. To compute deposition and mobilization rates for pregnant females between November and April, body reserves had to be calculated for the average pregnant female in November, which includes both lactating and non-lactating individuals. Body reserve for the average pregnant female in November was established as the average reserves in lactating and non-lactating females, weighted for the proportion of lactating and non-lactating females in the population, and for parturition rate in each lactation class. The proportion of non-lactating females in the population was established at 30% (Fancy et al. 1990) and an overall parturition rate of 82% was adopted (Fancy et al. 1990) (78.6% for lactating females, 90% for non-lactating females).

Stepwise multiple regression (SAS Institute 1985) was used to assess the effect of body composition on calf and fetal weight. Because calves were captured and weighed between June 3 and 6, calf weights were adjusted for capture date to correct for rapid neonatal growth. Calf weights were standardized to the mean calving date of June 4 using the growth rate of 275 g/d documented for bottle-fed caribou calves from the Porcupine Herd (Parker 1989).

Results

Sixty-eight female caribou were collected in 8 expeditions between 1987 and 1988 but 5 females were excluded from seasonal and reproductive comparisons because of under-age, Brucellosis infection, or questionable reproductive status. Of the remaining 63 females, 45 (71%) were reproductively-active at the time of capture (Table 1). In 1987, reproductively-inactive females were not collected in either March-April or June, and interannual comparisons were therefore precluded for this cohort during these periods. Of 10 radio-collared females that had calves experimentally removed in June 1987, 5 were successfully relocated and sacrificed.

Interannual Variation

Among reproductively-active females, interannual variations in body weight and composition were not statistically significant for any collection month (Table 2), and data for 1987 and 1988 were consequently pooled for statistical analyses. Percentage body fat was strikingly similar between the 2 years, differing by only 0.2 percentage point in June and September, and by 0.3 percentage point in March-April and November (Figure 1). Percentage body protein was also similar between the 2 years during September and November, but was significantly lower in 1987 than 1988 for March-April and June (Figure 1).

Among reproductively-inactive females, interannual variations in body weight, body protein, and body ash were not statistically significant (Table 3). However, a significant year-by-season interaction for carcass+viscera weight and body fat

Table 1. Sample size of female caribou collected during 1987 and 1988.

	MAR-APR	JUNE	SEPT	NOV	
Reproductively-active					
1987	7	5	5	6	
1988	9	7	2	4	
	16	12	7	10	Total: 45
Reproductively-inactive					
1987	0	0	2	4	
1988	1	5	3	3	
	1	5	5	7	Total: 18

Table 2. Interannual comparison of weight and composition for reproductively-active caribou females. Differences between 1987 and 1988 were not statistically significant for any parameter for any collection month (means shown ± 1 standard error).

	MAR-APR	JUNE	SEPT	NOV
Body Weight (kg)				
1987	88.6 ± 1.8	83.2 ± 0.4	97.4 ± 3.5	87.5 ± 3.2
1988	87.9 ± 3.6	91.7 ± 1.6	97.7 ± 7.0	90.9 ± 1.8
Carcass+Viscera Weight (kg)				
1987	56.9 ± 1.3	48.6 ± 1.0	56.6 ± 2.1	51.9 ± 1.6
1988	53.0 ± 1.6	50.1 ± 0.9	54.7 ± 1.7	54.0 ± 1.6
Body Fat (kg)				
1987	6.5 ± 0.5	2.8 ± 0.6	4.1 ± 0.6	4.5 ± 0.8
1988	5.8 ± 0.4	3.0 ± 0.3	4.1 ± 0.2	4.5 ± 0.4
Body Protein (kg)				
1987	9.3 ± 0.3	8.0 ± 0.3	11.6 ± 0.5	9.5 ± 0.4
1988	9.6 ± 0.3	8.9 ± 0.2	10.9 ± 0.6	10.2 ± 0.3
Body Ash (kg)				
1987	2.8 ± 0.1	3.0 ± 0.1	3.3 ± 0.4	2.8 ± 0.2
1988	3.1 ± 0.1	2.8 ± 0.1	3.4 ± 0.5	3.3 ± 0.1

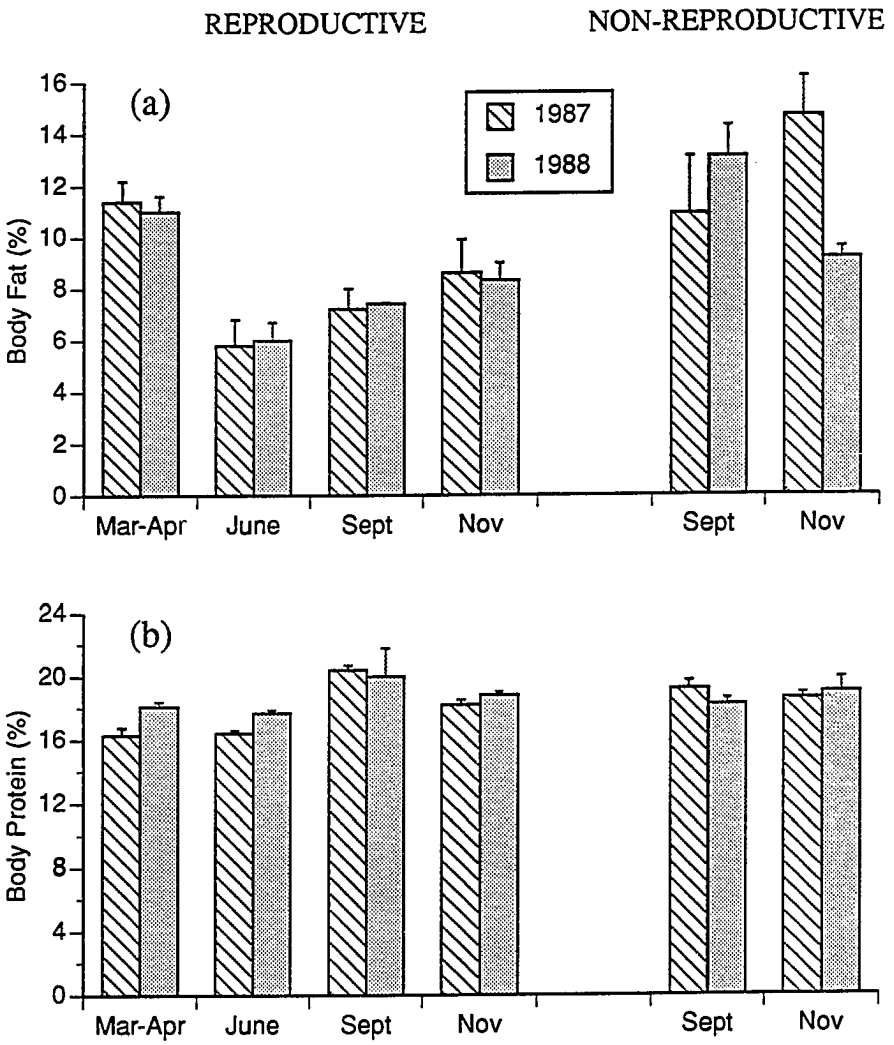

Figure 1. Interannual variation in (a) body fat and (b) body protein (%) in reproductively-active and reproductively-inactive female caribou.

Table 3. Interannual comparison of weight and composition for reproductively-inactive caribou females. Differences between 1987 and 1988 were not statistically significant for any parameter for any collection month. (Means shown ± 1 standard error). However, a significant year-by-season interaction was observed for carcass+viscera weight and body fat.

		SEPT	NOV
Body Weight (kg)			
	1987	97.7 ± 6.7	102.7 ± 3.1
	1988	109.3 ± 5.2	94.3 ± 1.6
Carcass+Viscera Weight (kg)			
	1987	60.5 ± 5.6	68.1 ± 1.7
	1988	70.1 ± 1.3	58.6 ± 0.8
Body Fat (kg)			
	1987	6.70 ± 1.92	10.02 ± 0.98
	1988	9.19 ± 0.87	5.43 ± 0.31
Body Protein (kg)			
	1987	11.61 ± 0.77	12.65 ± 0.46
	1988	12.74 ± 0.34	11.10 ± 0.37
Body Ash (kg)			
	1987	3.68 ± 0.81	3.96 ± 0.25
	1988	4.81 ± 0.67	3.70 ± 0.16

precluded the pooling of 1987 and 1988 data for these 2 components. Interannual variation in percentage body protein was comparable to that of the other cohort. However, interannual variation in percentage body fat was pronounced, especially in November when the mean difference equalled 5.5 percentage points (Figure 1).

Weights and compositions of gravid uteri in March-April did not differ significantly between 1987 and 1988 (Table 4). When data were pooled for the 2 years, the gravid uterus averaged 6.1 kg (Table 4) and represented 6.9% of mean maternal body weight. However, mean fat content in the gravid uterus equalled only 0.7 kg, while mean protein content equalled only 0.55 kg (Table 4). This contrasts with the 6.1 kg fat and 9.5 kg protein in maternal body reserves at this time.

Variations Between Seasons And Reproductive Cohorts

Body and Carcass+Viscera Weight

Body weights in reproductively-active females were stable throughout much of the year at 88 to 89 kg, but increased significantly in September by about 10% (Figure 2). Body weights in reproductively-inactive females also peaked in September (Figure 2) but seasonal changes were much more pronounced and ranged from 78 kg in March-April to 105 kg in September. Additionally, body weights did not decline significantly between September and November as in the other cohort.

Carcass+viscera weight in reproductively-active females averaged 56 to 62% of body weight and peaked at 52.7 kg in September after an annual low of 49.5 kg in June (Figure 2). Among reproductively-inactive females, carcass+viscera weight averaged 60 to 66% of body weight, and approximated the body weight pattern of

Table 4. Weight and calculated fat, protein, and ash content of gravid uteri in March-April.

	Mean	Minimum	Maximum	Std Error
1987 (n=8)				
Weight (kg)	5.68	4.50	6.56	0.262
Fat (kg)	0.07	0.05	0.08	0.003
Protein (kg)	0.51	0.40	0.59	0.023
Ash (kg)	0.11	0.08	0.12	0.005
1988 (n=8)				
Weight (kg)	6.47	4.99	8.62	0.356
Fat (kg)	0.08	0.06	0.10	0.004
Protein (kg)	0.58	0.45	0.77	0.032
Ash (kg)	0.12	0.09	0.16	0.007
1987 and 1988 pooled (n=17)				
Weight (kg)	6.10	4.50	8.62	0.239
Fat (kg)	0.07	0.05	0.10	0.003
Protein (kg)	0.55	0.40	0.77	0.021
Ash (kg)	0.11	0.08	0.16	0.004

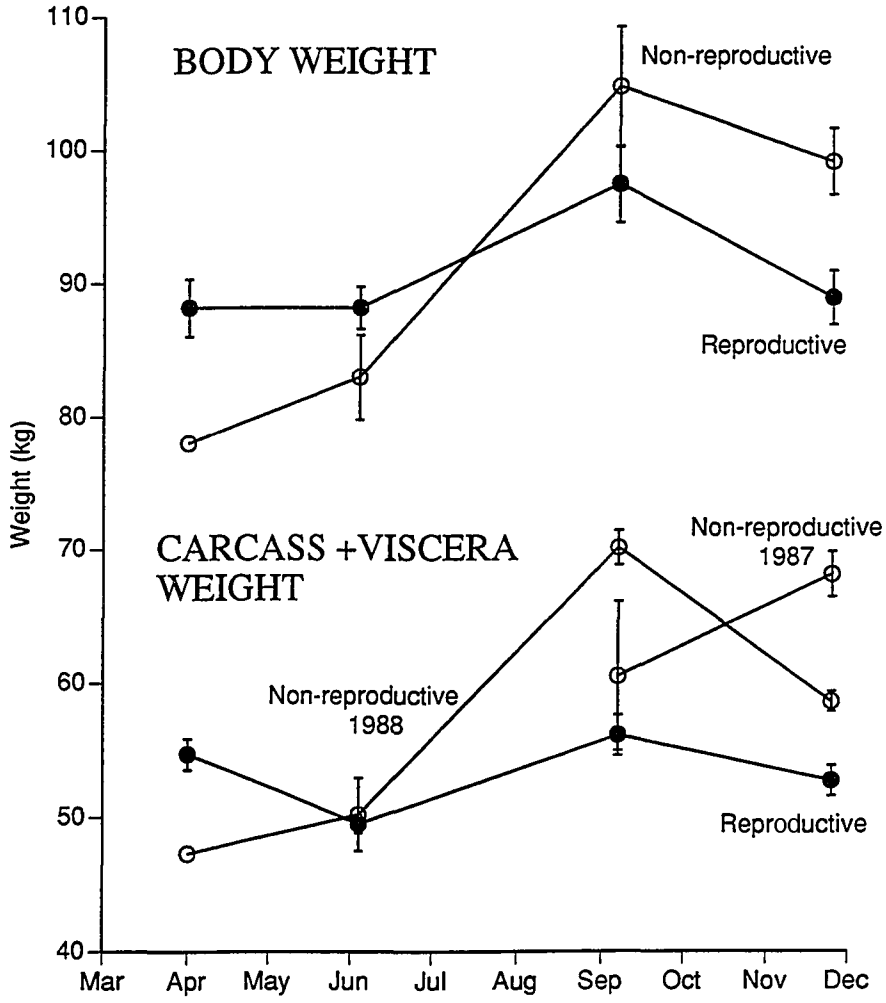

Figure 2. Seasonal body and carcass+viscera weights (kg) for reproductively-active and reproductively-inactive female caribou. 1987 and 1988 data pooled for carcass+viscera weight of reproductively-active females, and for body weights of both reproductive cohorts.

seasonal lows in mid and late winter, and seasonal highs in fall and early winter (Figure 2). However, a significant year-by-season interaction revealed opposing changes between September and November, with a non-significant increase in 1987 contrasting with a significant decline over the same period in 1988.

Comparison of reproductively-active and reproductively-inactive females (Figure 2) revealed significant body weight differences only in November. Similarly, only November differences in carcass+viscera weight were significant for both 1987 and 1988. Although carcass+viscera weight of reproductively-inactive females exceeded that of the other cohort in both September 1987 and September 1988, the difference was significant only in the second year.

Body Fat

Body fat reserves changed markedly during the year for both reproductively-active and reproductively-inactive females, but seasonal changes followed distinctly different patterns for these two cohorts (Figure 3). Among reproductively-active females, fat reserves declined by more than half during late gestation, from a peak of 6.1 kg in March-April to a low of 2.9 kg in June. Fat reserves increased following calving but gained only 1.6 kg between June and late November. Among reproductively-inactive females, seasonal changes in body fat were especially pronounced, with fat weight increasing 340% between April and September 1988 (Figure 3; Table 2). Following September, a significant decrease in fat weight contrasted with a significant increase in 1987 during the same period. As a result, peak fatness in 1987 occurred after peak fatness in 1988, even though maximum fat

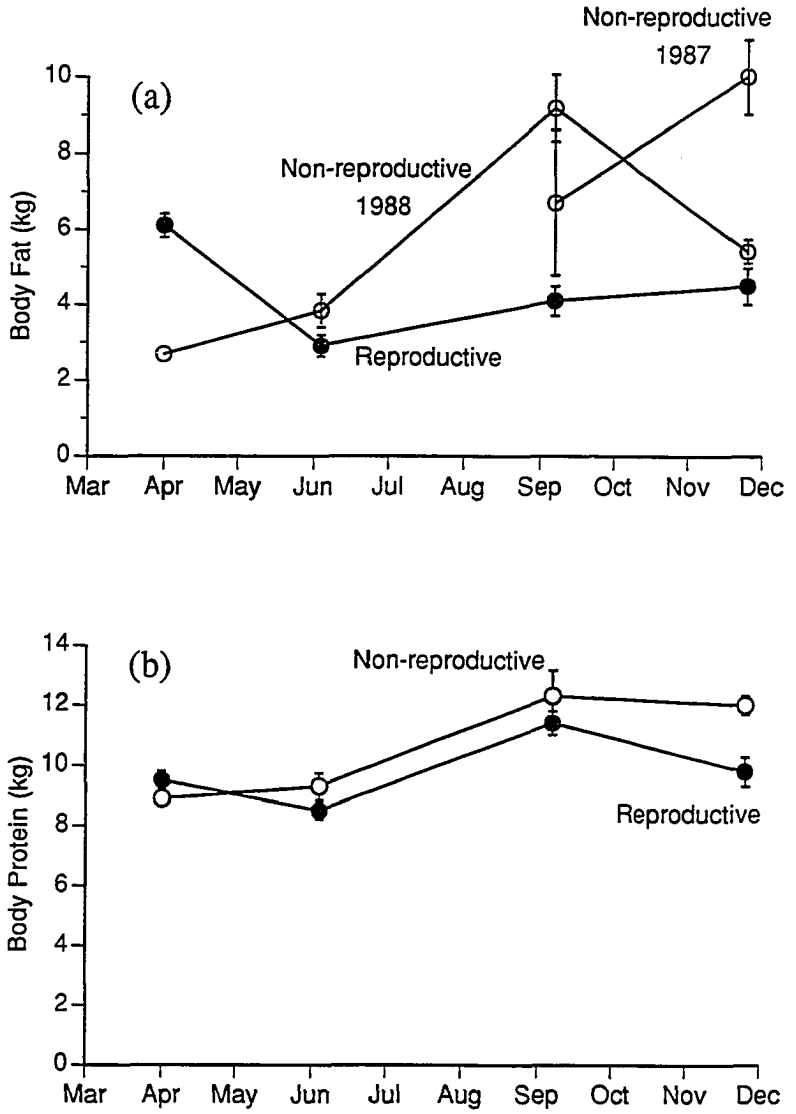

Figure 3. Seasonal (a) body fat and (b) body protein (kg) for reproductively-active and reproductively-inactive female caribou. 1987 and 1988 data pooled for body fat of reproductively-active females, and for body protein of both reproductive cohorts.

weights did not differ significantly between the 2 years, at 9.2 and 10.0 kg for 1987 and 1988 respectively.

Differences between the two reproductive cohorts were significant in November 1987, March-April 1988, and September 1988. Inter-cohort differences were especially pronounced in September 1988 and November 1987, when fat reserves in inactive females outweighed those in active females by more than 220%.

Body Protein

In contrast to seasonal changes in fat reserves, seasonal changes in protein reserves were relatively modest, ranging between 8.5 and 11.4 kg in reproductively-active females, and between 8.9 and 12.3 kg in reproductively-inactive females (Figure 3). Additionally, seasonal protein changes were similar between the 2 reproductive cohorts, with low values in mid and late winter increasing to high values in fall and early winter. Differences between the 2 cohorts were not significant with the exception of November, and even then, the difference equalled only 2.2 kg, or approximately 10% of the mean.

Body Ash

Body ash did not change significantly with season among reproductively-active females, even though mean values in September (3.3 kg) exceeded mean values at other times (3.0 kg in June, 2.9 kg in both March-April and November). Among reproductively-inactive females, body ash was significantly higher in September (4.4 kg) and November (3.8 kg) than in March-April and June (2.9 kg for both seasons).

Differences between the 2 reproductive cohorts were not significant with the exception of November.

Deposition and Mobilization Rates

Body reserves in reproductively-active females were rapidly mobilized during late gestation, with fat and protein losses averaging 50.1 and 15.4 g/d respectively between March and June (Figure 4). Following calving, fat and protein reserves were replenished between June and September, but protein deposition proceeded at 2.5 times the rate of fat deposition. The propensity for protein deposition was reversed between September and November, when fat deposition continued despite a rapid depletion in protein reserves. Between November and March, both fat and protein reserves were mobilized, but protein reserves continued to be depleted at a faster rate.

Among reproductively-inactive females, deposition of body reserves was rapid between June and September, averaging 53.0 g/d for body fat and 34.6 g/d for body protein (Figure 4). Between September and November, body reserve dynamics differed significantly between 1987 and 1988. In 1987, both fat and protein reserves were deposited during this period, with the rate of fat deposition exceeding the rate of protein deposition, as in the preceding interval. In contrast, both fat and protein reserves were mobilized during this same period in 1988, with the loss of fat reserves exceeding the loss of protein reserves. Between November and March, fat and protein reserves were mobilized at roughly equivalent rates.

The two reproductive cohorts therefore coincided in the period of maximum tissue deposition but diverged in other aspects of tissue dynamics (Figure 4). Whereas reproductively-active females preferentially deposited protein reserves between June

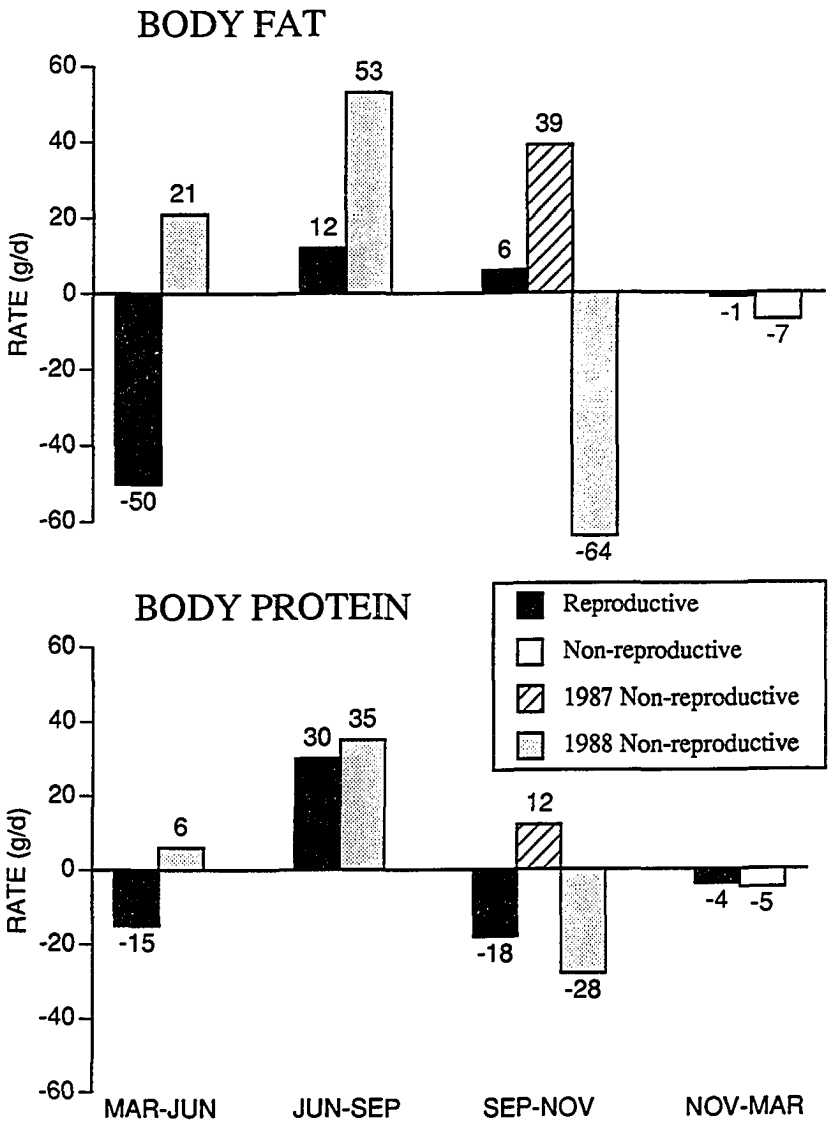

Figure 4. Deposition and mobilization rates for body fat and body protein in female caribou. November to March values are computed (see text). 1987 and 1988 data pooled for reproductively-active females.

and September, reproductively-inactive females preferentially deposited fat reserves. As a result, reproductively-inactive females deposited 330% more fat, but only 20% more protein, than their reproductive counterparts during this period. Among reproductively-inactive females, movements of fat and protein reserves were correlated, with concurrent depositions or mobilizations occurring throughout the year. In contrast, movements of fat and protein reserves in reproductively-active females may occur in opposite directions. Among reproductively-inactive females, changes in fat reserves were consistently faster than changes in protein reserves during both deposition and mobilization phases. In contrast, changes in fat reserves in reproductively-active females may be either faster or slower than changes in protein reserves.

Effects of Lactational Pause

Radio-collared female caribou that had experienced a lactational pause following experimental removal of their calves in June 1987 accumulated 140% more body fat and 33% more body protein than their lactating counterparts by November 1987 ($p<0.01$) (Figure 5). Radio-collared females that were recaptured and sacrificed in April and June 1988 had comparable body reserves to other pregnant females.

Effects on Reproductive Potential

Conception

In November, female caribou that successfully conceived several weeks earlier

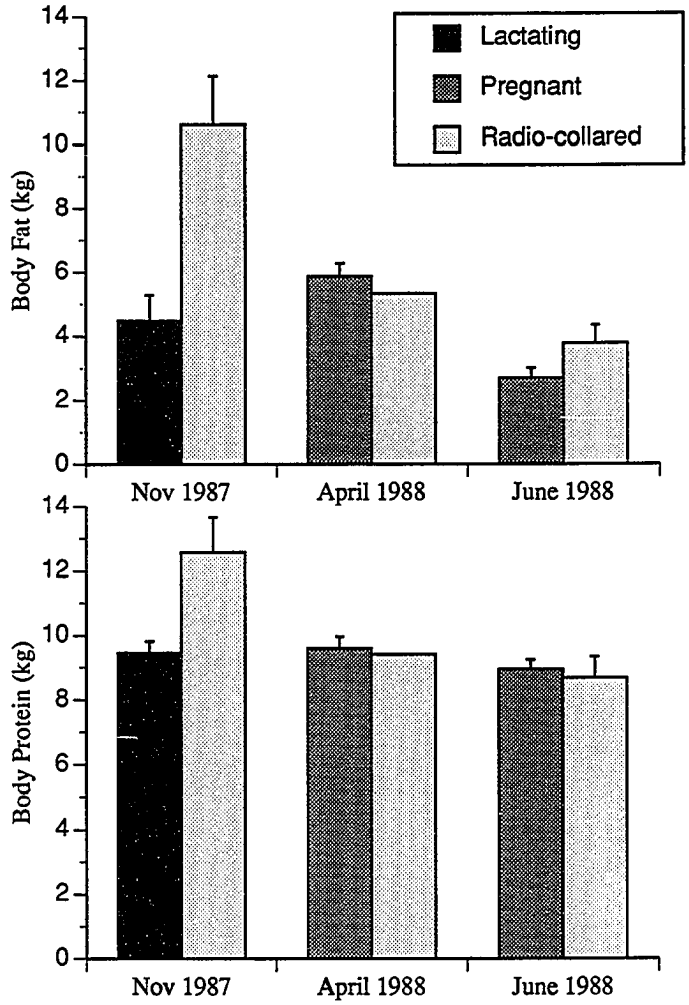

Figure 5. Comparison of fat and protein reserves between reproductively-active females and radio-collared females that had experienced a lactational pause in summer 1987. Lactating females are known to have lactated between June and November 1987. Pregnant females were randomly shot and probably lactated throughout summer 1987 (Fancy et al. 1990). Radio-collared females did not lactate in 1987 but are pregnant in April and June 1988.

were heavier and had 220% more fat and 17% more protein reserves than those that had not conceived (Table 5). However, these differences were not statistically significant, perhaps because the sample size was very limited. Pregnancy status was undeterminable from visual inspection in November 1988 and therefore, comparisons were limited to 7 pregnant and 2 barren individuals collected in November 1987.

The link between body reserves and successful conception may be strengthened by discounting extremely young individuals. The contribution of inexperience to reproductive failure is suggested by a 3.5 year old barren individual that had comparable fat and protein reserves to several pregnant females (Table 5). In contrast, a barren 11.5 year old female had 78% less fat reserves than either the average pregnant female or another pregnant female of the same age (Table 5). Additionally, the 1.7 kg body fat in this barren individual fell far below the lower limit of observed fat reserves in pregnant females (4.1 to 12.1 kg body fat; Table 5). This further emphasizes the critical role of body composition in the reproductive failure of this older individual.

Fetal Weight

Fetal weight (y; kg) in March-April was significantly affected by femur weight (x_1; g) and by weight of maternal protein reserves not adjusted for skeletal dimension (x_2; kg), according to the equation:

$$y = 1.72 - 0.00866\, x_1 + 0.4325\, x_2$$

(r^2=0.77; n=16; $p<0.01$). Fetal weight was not significantly affected by body weight, carcass+viscera weight, fat reserves, or ash weight.

Table 5. Comparison of body weights and compositions between pregnant and barren female caribou in November.

	Mean	Minimum	Maximum	Std Error
Pregnant (n=8)				
Body weight (kg)	94.3	81.3	109.5	3.7
Carc+visc weight (kg)	60.1	48.5	71.5	3.3
Body fat (kg)	7.5	4.1	12.1	1.1
Body protein (kg)	11.1	8.5	13.6	0.7
Age (yrs)	7.6	3.5	11.5	1.0
Barren (n=2)				
Body weight (kg)	90.7	81.0	100.5	9.7
Carc+visc weight (kg)	51.3	49.0	53.5	2.3
Body fat (kg)	3.4	1.7	5.1	1.7
Body protein (kg)	9.5	9.1	9.8	0.4
Age (yrs)	7.5	3.5	11.5	4.0

Birth Weight

Birth weight (y, kg) was significantly affected by weight of maternal protein reserves not adjusted for skeletal dimension (x, where $x > 7$kg) (Figure 6). This relationship was curvilinear and followed the equation:

$$y = 40.0 - 8.9527\,x + 0.5997\,x^2.$$

Birth weight was not related to body weight, carcass+viscera weight, fat reserves, or ash weight of the cow at parturition.

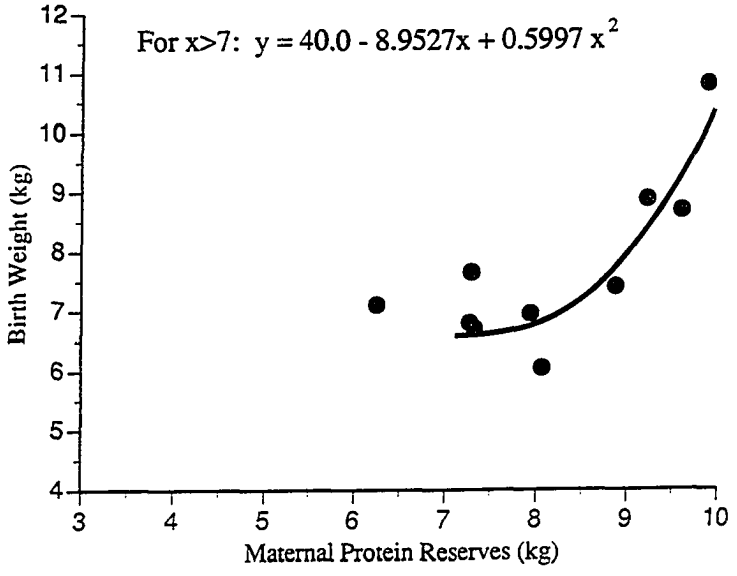

Figure 6. Relationship between calf birth weight (kg) and maternal protein reserves (kg) at parturition.

Discussion

Reproductively-active and reproductively-inactive female caribou exhibited distinct differences in body reserve dynamics as a result of their different nutritional commitments. Between March and June, the exponentially increasing costs of third trimester gestation (Roine et al. 1982, Robbins and Moen 1975) lead to rapid tissue catabolism among pregnant females. During this period, body reserve dynamics for non-pregnant females were unclear because of the single March sample, but the limited data indicated an accumulation of body reserves. Between June and September, both reproductive cohorts deposited body tissue in response to an abundance of high quality forage. However, lactating females were seriously compromised in their ability to replenish body reserves, and accumulated only 20% as much fat, and 90% as much protein, as non-lactating individuals. The compromise to maternal body reserves is not surprising given costly lactational expenditures that may average 10 MJ/d (Parker et al. 1990). A milk energy output of this magnitude would effectively increase energy requirements by 50 to 60% above a fasting metabolism of approximately 18 MJ/d (Fancy 1986).

Between June and September, the preferential deposition of body protein by lactating females contrasted with the preferential deposition of body fat by non-lactating females. However, these opposing tendencies can also be explained by the different nutritional burdens of the reproductive cohorts. In ruminants, allocation priorities for absorbed nutrients are firstly towards maintenance, then protein deposition, and finally towards fat deposition (Berg and Butterfield 1976, Byers 1982). In lactating females, a lower net availability of absorbed nutrients would therefore result in disproportionately less energy for adipose tissue following

maintenance, milk synthesis, and protein anabolism. In contrast, a large energy surplus in non-lactating females would lead to rapid fat deposition. Thus, as net available energy increases, the proportion of energy that is deposited as fat rather than protein also increases (McEwan and Whitehead 1970, Holter and Hayes 1977, Holter et al. 1979).

Between September and November, lactating females reversed their propensity for protein deposition and preferentially deposited adipose tissue while mobilizing protein reserves. This reversal in favor of fat deposition may be partly due to the effects of a shortening fall photoperiod. A linkage between photoperiod and fat deposition has been demonstrated by Abbott et al. (1984), who found that white-tailed deer fawns exposed to short daylengths accumulated 4 times more fat than fawns exposed to long daylengths following a 9 week experimental period. Similarly, Larsen et al. (1985) concluded that lipogenic capacity in isolated adipocytes from Svalbard and Norwegian reindeer was highest in fall and lowest in winter. The reversal in deposition pattern may also be attributed to a seasonal change in forage protein, which in caribou diets may decline by more than 50% between June and September (Whitten and Cameron 1980, Boertje 1990). In contrast, dietary nonstructural carbohydrates remain relatively constant over this period (Whitten and Cameron 1980, Boertje 1990) and, coupled with the seasonal increase in lichen intake, allow for the continued deposition of body fat. The reversal in favor of fat deposition may even be a strategical measure by lactating females to deposit body fat at the expense of body protein by using amino acids as a carbon source. This would be an effective strategy to compensate reproductive expenditures since lactational demands greatly compromised fat deposition, but not protein deposition, over the summer. In ruminants, deaminated protein reserves may contribute 12-30% of the carbon required

for gluconeogenesis (MacRae and Lobley 1986), and the glucose thus produced could be used as an energy source for fat deposition. Alternatively, glucogenic amino acids may enter the pentose phosphate pathway and generate NADPH-reducing equivalents required for fatty acid synthesis (Van Soest 1982). Experimental work with sheep has shown that animals given phloridzin infusions, which cause urinary excretion of glucose, respond by increasing the conversion of amino acid carbon to glucose (Egan et al. 1983). Thus, ruminants can respond with increased protein deamination during periods of need, as might be the case for lactating caribou between September and November.

The opposing fat and protein dynamics exhibited by lactating females were not observed in non-lactating individuals. In 1987, non-lactating females deposited both fat and protein reserves between September and November, but mobilized both tissues during the same period in 1988. The correlated movements of fat and protein in non-lactating females during both deposition and mobilization phases suggest that these individuals are primarily responsive to current nutritional intake, and not to opposing and asynchronous changes in supply and demand. In contrast, lactating females must adroitly balance supply and demand for fat and protein in order to satisfy both reproductive expenditures as well as anticipated requirements over a prolonged winter. The selective pressure for lactating females to achieve seasonal target conditions is supported by the strikingly low interannual variation shown by this cohort during the 2 years of study. Evidence for set points in body weight has been previously forwarded for reindeer, (Ryg 1983), wapiti (Hudson et al. 1985), moose (Renecker and Hudson 1986), and mule deer (Renecker and Samuel 1991).

Diverging body compositions between reproductively-active and reproductively-inactive females only occurred in summer. In early winter, body

compositions converged between reproductive cohorts, with fat mobilization between November and March preceding at a faster rate in females that had not lactated the previous summer. The divergent effects of summer, and the convergent effects of winter, are clearly reflected in seasonal differences that were most pronounced in November, and least pronounced in June. In November, body weight, carcass+viscera weight, body fat, and body ash all differed significantly between the two reproductive cohorts for at least one of the 2 study years. In contrast, none of these weight and composition parameters were significantly different between the two reproductive cohorts in June in either of the 2 study years.

The convergent effects of early winter are also apparent among lactating females that had their calves experimentally removed in June 1987. Although these non-lactating females had accumulated more fat and protein reserves than their lactating counterparts by November, this advantage was no longer evident the following April and June. These results concur with those for red deer; Clutton-Brock et al. (1982) reported that body conditions did not differ between milk and yeld hinds in April even though yeld hinds had entered the winter with substantially higher fat reserves.

The convergence of body compositions between lactating and non-lactating females following September is intriguing, and has a number of possible explanations. One possibility is that the hormonal milieu of lactating females had carried over into early winter. Because reproductive hormones associated with lactation increase both physiological efficiency (Jumah et al. 1965, Ferrell 1988) and voluntary food intake (Forbes 1986), lactating females would be predisposed towards tissue deposition once milk output declined. A second possibility is that the lactating females were showing the compensatory growth that can occur after restricted nutrition. Such compensatory

growth is widespread among birds and mammals (Wilson and Osbourn 1960, Meyer and Clawson 1964, Renecker and Hudson 1986, Renecker and Samuel 1991), and has also been documented for both reindeer cows (Espmark 1980) and calves (Jacobsen et al. 1977, Ryg and Jacobsen 1982). A third, related possibility is that the non-lactating females had become metabolically inefficient after a summer of high quality forage and low energy demands, and their body reserves are rapidly depleted once forage quality declines. Excess fat may even be shed by non-lactating females because such reserves are metabolically expensive to maintain and do not confer any adaptive advantage. Finally, a fourth explanation is that non-lactating females that become pregnant willingly invest more heavily in their fetuses than their leaner, lactating counterparts, and therefore deplete their fat reserves at a faster rate. Non-lactating females may also be investing more heavily in their fetuses merely because they are more advanced in their gestation. An advanced gestation in fat, non-lactating females is supported by the earlier onset of seasonal breeding (Bronson 1989) and hastened parturition (Espmark 1980, Clutton-Brock et al. 1982, Reimers 1983a, Skogland 1983) characterizing well nourished individuals. Tyler (1987) previously suggested that pregnant Svalbard reindeer may preserve fat reserves during late gestation in anticipation of lactational demands. However, this hypothesis does not apply to female caribou in this study because pregnant females only reduced fat catabolism between November and March. Tissue catabolism in pregnant females greatly increased during late gestation, and exceeded that in non-pregnant females between March and June.

Circumstantial evidence from this study supports a linkage between body composition and conception rate in caribou. Body weight, carcass+viscera weight, body fat, and body protein were all higher in pregnant than barren females several

weeks after breeding. Differences between the reproductive cohorts were not statistically significant but this was probably due to an inadequate sample. Circumstantial evidence also suggests that age may be a factor in conception success, with inexperienced animals being less likely to conceive despite sexual maturity. Such inexperience may explain the lack of relationship between reproductive rate and body weight reported by Davis et al. (1991) for 2 year old female caribou. Additionally, the large variation in gastrointestinal content, particularly among young animals (Adamczewski et al. 1987), may have obliterated the relationship between body weight and body reserves, and hence, the relationship between body weight and conception rate. In this study, fat reserves in a mature, barren female fell dramatically below the range of values for pregnant individuals. This result is consistent with those reported by Dauphiné (1976) for mature female caribou, in which pregnant females in November and December averaged 5.3 times more back fat, 1.7 times more kidney fat, and 2.3 times more abdominal fat than barren individuals. Recent work on the Central Arctic Caribou Herd in northcentral Alaska (Cameron et al. 1991) also indicate a positive relationship between body weight and the probability of conception.

Fetal weight in March-April and birth weight in June significantly correlated with maternal protein reserves, but not maternal fat reserves, at the the time of collection. However, a lack of correlation between maternal fat reserves at the time of sampling and either fetal or birth weight does not preclude the importance of body fat in fetal development, since maternal fat reserves that may have existed at conception may already have been used for fetal growth. This is particularly true in this population where converging body compositions over winter resulted in low inter-individual variation in fat reserves by March-April. Nonetheless, the importance of

protein reserves to fetal development is underscored by the results which suggest that protein, rather than energy, may be the limiting factor in gestation. Such a hypothesis would concur with the energy rich but protein poor lichen diets characterizing winter caribou nutrition (Boertje 1990, Thomas and Hervieux, 1986, Russell and Martell 1984).

Seasonal fluctuations in body weight were less pronounced among female caribou of this population than among high-arctic reindeer in Svalbard, which experienced 50% weight reductions between August and May (Reimers and Ringberg 1983). Comparisons with other populations are more difficult because of differences in sampled cohorts, sampling season, or body weight definitions. However, it appears that seasonal weight changes in the Porcupine Herd were also less pronounced than in insular caribou on Coats Island (Adamczewski et al. 1987). Seasonal weight changes were more comparable to those of other North American mainland populations, including the George River Herd in northern Quebec (Huot 1989) and the Kaminuriak Herd east of Hudson Bay (Dauphiné 1976). Comparison of ingesta-free body weight differences between November and April (Table 6) confirm a larger seasonal weight change in insular than mainland caribou. However, ingesta-free body weights were reasonably similar among all populations (Table 6). Among reproductively-active females of the Porcupine Caribou Herd, a unique bimodal peak in carcass+viscera weight (Figure 2) reflected both the April peak in fat reserves and the September peak in protein reserves. This seasonal bimodal weight distribution was not observed in either the Coats Island or Kaminuriak populations where seasonal weight data were also available throughout the year.

Seasonal fluctuations in fat reserves were also less pronounced in this and other mainland populations (Dauphiné 1976, Huot 1989) when compared with those

Table 6. Comparison of ingesta-free body weight (kg) and fat composition (%) in adult female caribou in 4 North American populations. Data for the mainland populations are of lactating females in November and pregnant females in April (Kaminuriak data from Dauphine 1976; George River data from Huot 1989). Data for Coats Island are of females with mixed reproductive status (Adamczewski et al. 1987).

	INGESTA-FREE BODY WEIGHT[1] (kg)		BODY FAT[2] (%)	
	NOV	APR	NOV	APR
MAINLAND POPULATIONS				
Porcupine	75.9	72.3	8.5	11.2
Kaminuriak			15.6	12.4
George River	73.9	72.8	5.2	10.7
ISLAND POPULATION				
Coats Island	76.1	68.7	19.7	7.5

[1]Antler weight included for Coats Island population only.
[2]Percentage body fat for Kaminuriak and Coats Island estimated from kidney fat using regresssion equations from indices chapter.

in Svalbard reindeer (Reimers 1984) or caribou from Coats Island (Adamczewski et al. 1987). Additionally, fat composition in the mainland populations did not decline precipitously between November and April as on Coats Island (Table 6). In this study, percent body fat in pregnant females in April was similar to percent body fat in the average pregnant female in November. These results corroborate those of Huot (1989), who similarly concluded that caribou from the George River Herd were primarily protein and not energy limited between October and April.

In conclusion, the study results support the null hypothesis (Ho_1) of differential body reserve dynamics in reproductively-active and reproductively-inactive female caribou. The study results also support Ho_3 by demonstrating that fetal weight in March-April and birth weight in June were positively correlated to maternal protein reserves. However, neither fetal nor birth weight significantly correlated with maternal fat reserves. Additionally, there was insufficient evidence to support Ho_2 even though the limited data appear to corroborate a positive relationship between pregnancy rate and maternal body condition.

Chapter 2.

Effects of Dietary Protein and Energy on Body Reserve Deposition and Milk Production in Caribou and Reindeer

Introduction

Caribou and reindeer inhabiting the circumpolar arctic are constrained by extreme winter conditions that limit weight gain and tissue deposition to a short season (McEwan 1968, Dauphiné 1976, Reimers 1983a, White and Fancy 1986, Adamczewski et al. 1987, Chapter 1). During the brief summer, nutrient acquisition must satisfy conflicting requirements for maintenance, growth, and reproduction that demand different types of tissue production over different timeframes. In breeding females, nutrient partitioning during lactation allocates limited resources between milk production for the neonate and replenishment of maternal body reserves depleted over the prolonged winter. In both breeding and non-breeding females, nutrient partitioning also allocates substrates between fat and protein deposition. A partitioning strategy that balances trade-offs between dam and offspring, and between adipose tissue and lean muscle, is especially critical in caribou and reindeer in which reproductive success (Dauphiné 1976, Haukioja and Salovaara 1978, White 1983, Reimers 1983a, 1983b, Rognmo et al. 1983, Leader-Williams 1983, Skogland 1983, 1984, Cameron et al. 1991) and survival (Klein 1968, Thomas et al. 1976, Reimers et al. 1982) are strongly dependent on realized body composition.

Nutrient partitioning in *Rangifer tarandus* has received little study but research on other species indicate that deposition patterns are affected by dietary protein and

energy intake. In domestic ruminants, priorities for fat deposition increases with increasing energy intake and rate of growth (Berg and Butterfield 1976, Byers 1982, Byers and Schelling 1988). Similarly, fat deposition in white-tailed deer fawns was stimulated by high dietary energy, but depressed by high dietary protein (Holter and Hayes 1977, Holter et al. 1979). Circumstantial evidence on caribou and reindeer (McEwan and Whitehead 1970, Chapter 1) also suggest that the proportion of energy retained as fat rather than protein increases with increased energy availability.

For a given nutritional plane, deposition of fat and protein reserves is expected to differ between lactating and non-lactating females. During lactation, a series of metabolic adaptations promote the mobilization of fat reserves for milk production (Vernon and Flint 1984, Thornton 1987). Among free-ranging caribou, lactating females are seriously compromised in their ability to replenish body reserves between June and September, and only accumulated 20% as much body fat as non-lactating females (Chapter 1). However, lactating females may also experience compensatory growth following peak lactation and deposit more body tissue than non-lactating females in fall and early winter (Chapter 1). Such compensatory growth has been widely documented among both domestic and wild species following undernutrition (Wilson and Osbourn 1960, Meyer and Clawson 1964, Jacobsen et al. 1977, Espmark 1980, Ryg and Jacobsen 1982, Suttie et al. 1983, Renecker and Hudson 1986, Renecker and Samuel 1991).

Nutrient partitioning between fat and protein deposition may also be seasonally dependent. Lactating female caribou favored protein deposition between June and September but preferentially deposited body fat between September and November (Chapter 1). Increased lipogenesis in fall has also been suggested for other cervids (Verme and Ozoga 1980, Ryg 1986) and demonstrated for isolated adipocytes

from Svalbard and Norwegian reindeer (Larsen et al. 1985). Such seasonal changes in tissue deposition may be attributed to seasonal changes in energy and nutrient intake, but may also be linked to a declining photoperiod (Abbott et al. 1984).

Nutrient partitioning between maternal body reserves and milk production may be similarly dependent on season. In reindeer, restricted nutrition following peak lactation resulted in reduced milk yield and calf growth but did not affect maternal body weight (White 1983, White and Luick 1984). Similarly, restricted nutrition following parturition strongly affected maternal body weight in red deer up to 40 days post-partum, but had little effect subsequently (Loudon et al. 1984). These studies suggest that priorities for milk production may decline as the season progresses and the calf ages.

The objective of this study is to determine the effects of dietary protein and energy, and the dietary protein:energy ratio, on the deposition of body fat and body protein in caribou (*Rangifer tarandus granti*) and reindeer (*Rangifer tarandus tarandus*). Nutritional effects and deposition patterns will be compared between lactating and non-lactating individuals, and nutrient partitioning between milk production and maternal tissue deposition will also be examined for lactating females. Null hypotheses being tested are:

Ho_1: The proportion of tissue deposited as fat rather than protein will

(a) increase with increased energy intake.;

(b) decrease with increased protein intake;

(c) decrease with an increased protein:energy ratio;

(d) increase between spring and fall; and

(e) decrease with increasing fatness.

Ho_2: Nutrient partitioning between milk production and maternal tissue deposition will be a function of

(a) maternal energy intake;

(b) maternal protein intake;

(c) maternal dietary protein:energy ratio;

(d) calf age; and

(e) maternal body condition.

Methods

This study was conducted at the Large Animal Research Station of the Institute of Arctic Biology, University of Alaska Fairbanks, using eight female caribou and nine female reindeer. Four diet treatments varying in the protein:energy ratio were formulated to give 2 levels of energy and 2 levels of protein (Table 7). The high protein:high energy diet (H*p*H*e*) and the low protein:high energy diet (L*p*H*e*) were formulated for 78% digestible energy, with 20 and 10% crude protein respectively. The high protein:low energy diet (H*p*L*e*) and the low protein:low energy diet (L*p*L*e*) were also formulated for 20 and 10% crude protein respectively, but at only 50% digestible energy. The four diets were randomly assigned within each group of 4 lactating caribou, 4 lactating reindeer, 4 non-lactating caribou, and 4 non-lactating reindeer. A fifth non-lactating reindeer was assigned the low protein:low energy diet. Pregnancies were terminated in non-lactating reindeer 30 days after mating by intramuscular injection of 2 ml Estrumate (Miles Laboratories Inc., Shawnee, KS); non-lactating caribou had not been mated. All animals were either penned individually or, in the case of lactating females, as a cow:calf pair. Experimental diets were offered as pelleted rations together with pre-mixed, unpelleted ingredients to provide roughage and promote maximal feeding. A pre-experimental period (2 weeks for caribou; 8 weeks for reindeer) provided time for habituation to the pens and diets. Feed analyses of both pelleted rations and raw ingredients were conducted to confirm nutrient content (Triple "S" Lab, Inc., CO). Feed was offered ad libitum, and feed intake and composition were monitored on a daily basis for each animal. Each calf had access to a creep feeder that was barred from the cow, and offered ad libitum a common high protein, high energy diet.

Table 7. Composition (%) and nutritional content of pelleted experimental rations.

	H_pH_e	L_pH_e	H_pL_e	L_pL_e
Ingredients				
Barley	33.2	23.8	0.6	24.4
Corn	17.5	43.0		
Soybean meal	14.4		35.0	2.5
Meat meal	5.0			
Beet pulp	15.0	25.0	25.0	25.0
Hay			6.2	6.2
Molasses	10.0	5.0	5.0	5.0
Fibre-lite			25.0	25.0
Wheat screenings				8.8
Vitamin premix	0.2	0.2	0.2	0.2
Tallow	1.8			
Sodium bentonite	1.0	1.2	1.2	1.2
Other[1]	1.7	1.8	1.7	1.7
Nutritional content[2]				
Moisture (%)	8.8	8.6	7.2	7.8
Total protein (%)	17.8	10.0	20.1	10.0
Digestible protein (%)	14.0	7.8	13.3	6.5
Crude fat (%)	5.1	4.1	1.7	1.6
Crude fiber (%)	5.5	6.1	19.5	21.1
Ash (%)	6.6	6.4	6.9	6.2
Nitrogen free extract (%)	56.2	64.8	44.7	53.3
TDN (%)	81.6	78.4	50.5	47.5
Net energy (MJ/kg)	7.6	7.3	4.3	4.0

[1]Other ingredients include dicalcium phosphate, trace minerals, salt, and flavor.
[2]Nutrient analyses conducted by Triple "S" Lab Inc., CO.

The experiment began May 24th, two to four weeks after calving, and continued for 12 weeks. Animals were weighed every third day and body composition determined every third week using the tritiated water (TOH) technique (Holleman et al. 1982). At the start of each TOH trial, a pre-injection blood sample was drawn from the jugular vein and then 1 ml TOH was injected intramuscularly. The dose concentrations of 1 mCi/ml for lactating females and 200 uCi/ml for non-lactating females were made from a stock solution of 100 mCi/ml (NET-001D; New England Nuclear Research Products, Boston, MA) diluted with physiological saline. Four to five post-injection urine samples were obtained, beginning 1 day post-injection and subsequently at 2-3 day intervals. Urine samples were collected during voluntary urination with a vial attached to the end of a 2 m pole. Infrequently, urine samples could not be collected and were substituted with blood samples obtained by venipuncture. All blood samples were immediately centrifuged and the plasma separated. Urine and plasma samples were then stored at -20C until subsequent analyses.

Water was separated from plasma and urine samples by lyophilization and prepared for radioassay of TOH. Each water sample (1 ml) was mixed with Ecolume scintillation solution (8 ml) (ICN Biomedicals, Inc., Irvine, CA) and counted for 3-10 min periods on a Beckmann LS-7500 Liquid Scintillation System using external standardization (LS window 0 to 18.5 KeV). The equilibrium specific activity of TOH was determined by extrapolation to time zero using least squares regression of post-injection specific activity versus time (Holleman et al. 1982). The total body water space (TBWS; ml) was calculated using the equation (Holleman et al. 1982):

$$TBWS = D/Se - V_D \quad (1)$$

where: D=dose (dpm)

Se=equilibrium specific activity (dpm/ml)

V_D=volume of dose (ml)

TBWS was subsequently reduced by 10% to correct for the overestimation of total body water using the tritiated technique (Sheng and Huggins 1979, Fancy et al. 1986). Body fat composition was computed from TBWS using a regression equation based on summer and fall data collected on female caribou from the Porcupine herd (Figure 7a). Body protein composition was computed as a function of the ingesta-free, fat-free body weight using a regression equation based on the same population (Figure 7b). A ratio of lean tissue to dry protein, previously determined as 5.00 (Indices chapter), was used to calculate lean body mass.

Milk intake of calves was determined in conjunction with TOH trials at 3 week intervals using the double isotope technique (Holleman et al. 1975, 1988). Following the collection of a pre-administration blood sample, a single dose of deuterium oxide (D_2O) (1ml/kg body weight; Aldrich Chemical Co., Milwaukee, WI) was orally administered to each calf. Post-administration urine samples were collected from the calves using the same time schedule and technique as for the cows.

Plasma and urine samples from the calves were lyophilized and analysed for both TOH-specific radioactivity as well as D_2O concentration. D_2O concentration was determined using a Foxboro Miran I infrared spectrophotometer set at a wavenumber of 2487 cm^{-1} (Thornton and Condon 1950, Gaunt 1956). The time between infusion of a sample into the spectrophotometer and its reading was standardized to avoid changes in absorbance characteristics caused by equipment heating of the sample (Zweens et al. 1980).

A two compartment model was used to determine water turnover in the calf and milk water transfer from cow to calf (Figure 8). The model was solved

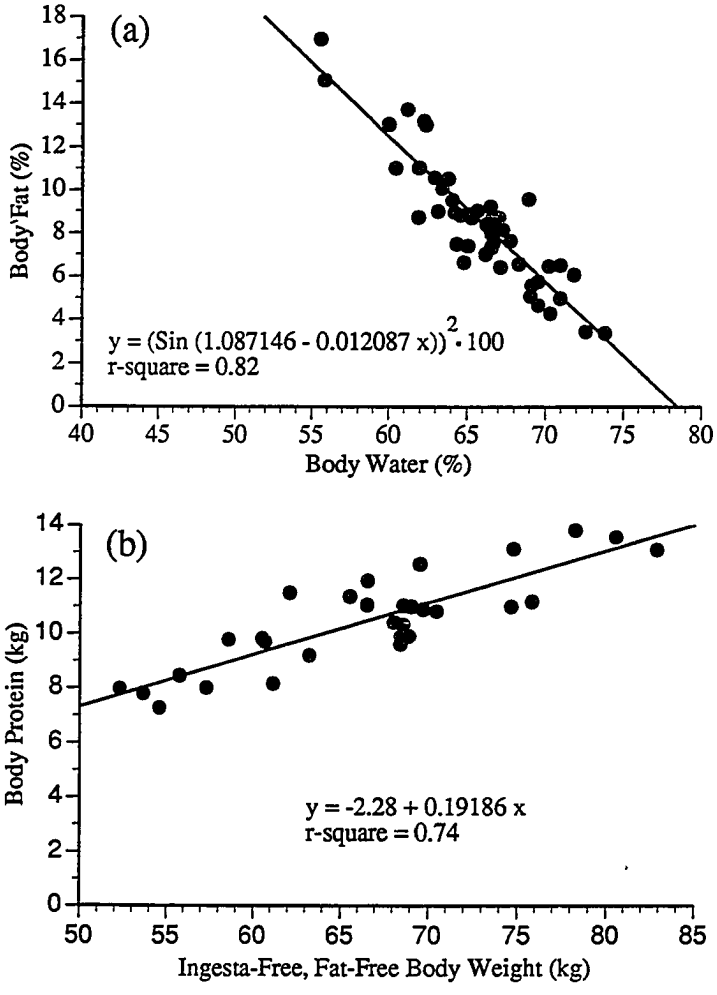

Figure 7. (a) Regression between body water (%) and body fat (%) in adult female caribou. (b) Regression between body crude protein (kg) and ingesta-free, fat-free body weight (kg) in adult female caribou. Both regressions based on summer and fall data for adult female caribou from the Porcupine herd.

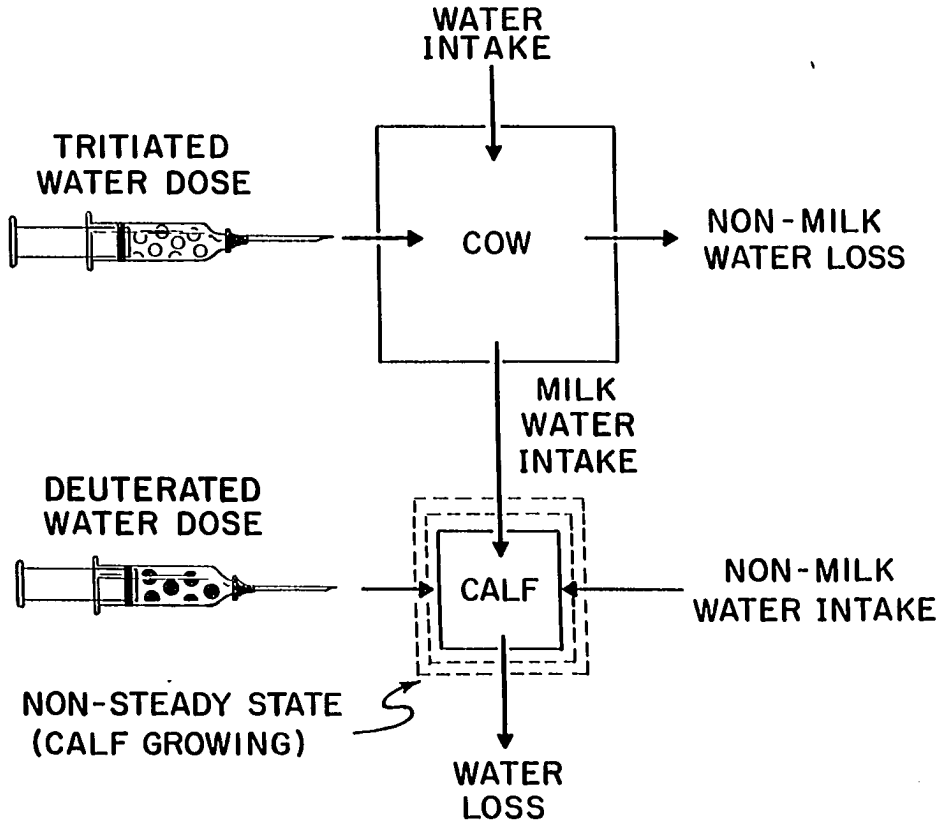

Figure 8. The 2 compartment model used to compute water turnover rate in the calf and the water transfer rate between cow and calf (Holleman et al. 1988).

analytically using an interactive version (CONSAM 30.1) of the Simulation, Analysis and Modelling program (SAAM27; Berman et al. 1983). A solution for milk water intake was derived by optimizing the fit between model kinetic parameters and observed tracer concentrations, while allowing for the continual growth of the calf (Holleman et al. 1988).

Lactating females were hand milked on the 6th and 12th week of the experiment following intramuscular injection of 1 ml oxytocin. Dry matter content of milk samples was determined by lyophilization, and used to calculate milk intake from milk water intake. Fat content of milk solids was determined by petroleum-ether extraction. Protein content was analyzed as kjeldahl nitrogen (AOAC 1984) multiplied by a specific factor of 6.38 (Maynard et al. 1979). Defatted, dry milk samples were dissolved in water and the non-soluble solids separated out. Anthrone (0.2% in 95% sulfuric acid) was added to the remaining liquid and lactose concentration determined from standard curves using a Beckman DB-G Grating spectrophotometer set at a wavelength of 665 nm. Energy content of milk solids was determined by bomb calorimetry (Wildlife Habitat Lab, WSU).

Stepwise multiple regression (SAS Institute Inc. 1989) was used to assess the effects of protein intake, energy intake, the dietary protein:energy ratio, time interval, and body condition on weight gain, fat and protein deposition, and milk production. Number of days post-partum was also an independent variable in regressions of milk parameters. Protein and energy intakes were expressed both as absolute amounts and on a per metabolic weight basis. Body condition was defined as percent body fat at the beginning of each body composition trial, while time interval was defined by each 3-week trial period. Significance level was established at $p<0.05$.

Results

Chronological Changes

Body Weight

Body weight changes over the experimental period varied dramatically between individuals, ranging from a net loss of 6.4 kg to a net gain of 31.1 kg (Figures 9 and 10). All caribou registered weight gains by the end of the 12 week period regardless of lactational status. However, two lactating reindeer suffered weight losses that were not compensated by the end of the experiment, while 1 non-lactating reindeer accumulated a net gain of only 2.2 kg. For most animals, body weight gains were most rapid following mid-July. Some individuals also gained weight rapidly in June but much of these gains were negated in early July when hot weather depressed appetite drive and feed intake.

Lactating caribou and reindeer averaged only 71 and 47 percent of net weight gains for non-lactating caribou and reindeer respectively. However, the maximum weight gain experienced by any single individual did not differ greatly between lactation class or subspecies, equalling 24.7 kg for a lactating caribou, 29.3 kg for a lactating reindeer, 31.1 kg for a non-lactating caribou, and 25.6 kg for a non-lactating reindeer (Figures 9 and 10).

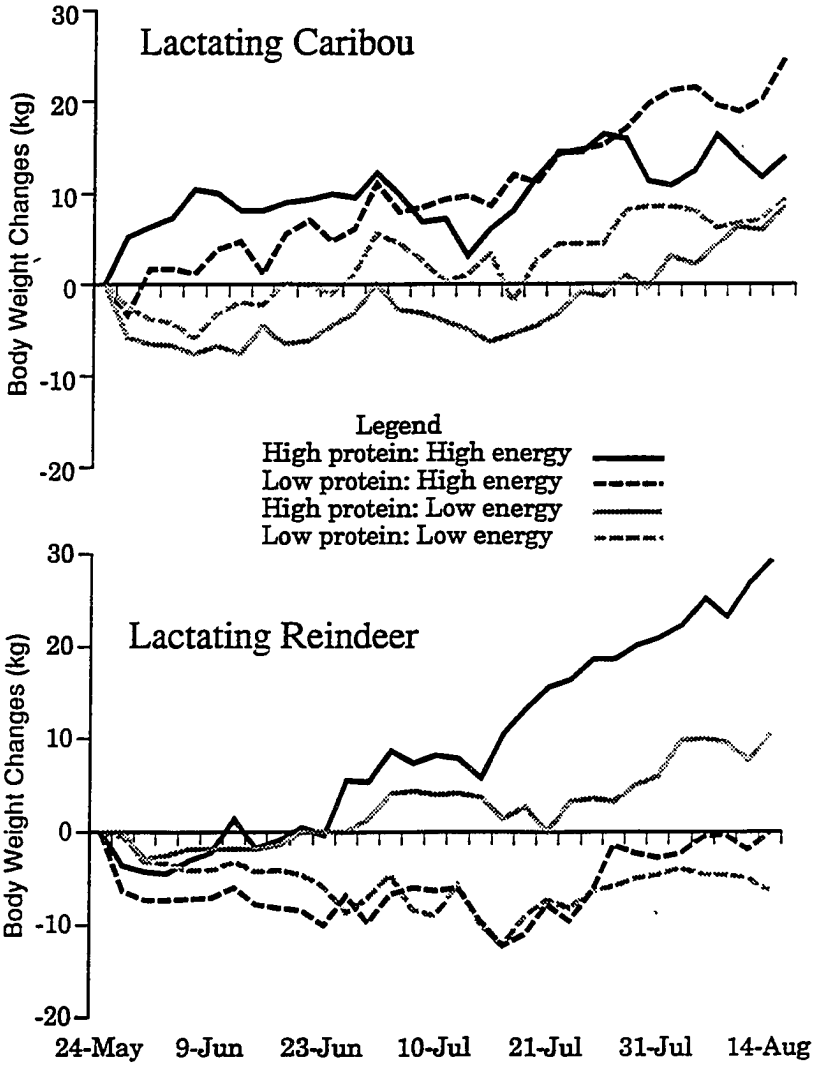

Figure 9. Body weight changes (kg) in individual lactating caribou and reindeer over the experimental period.

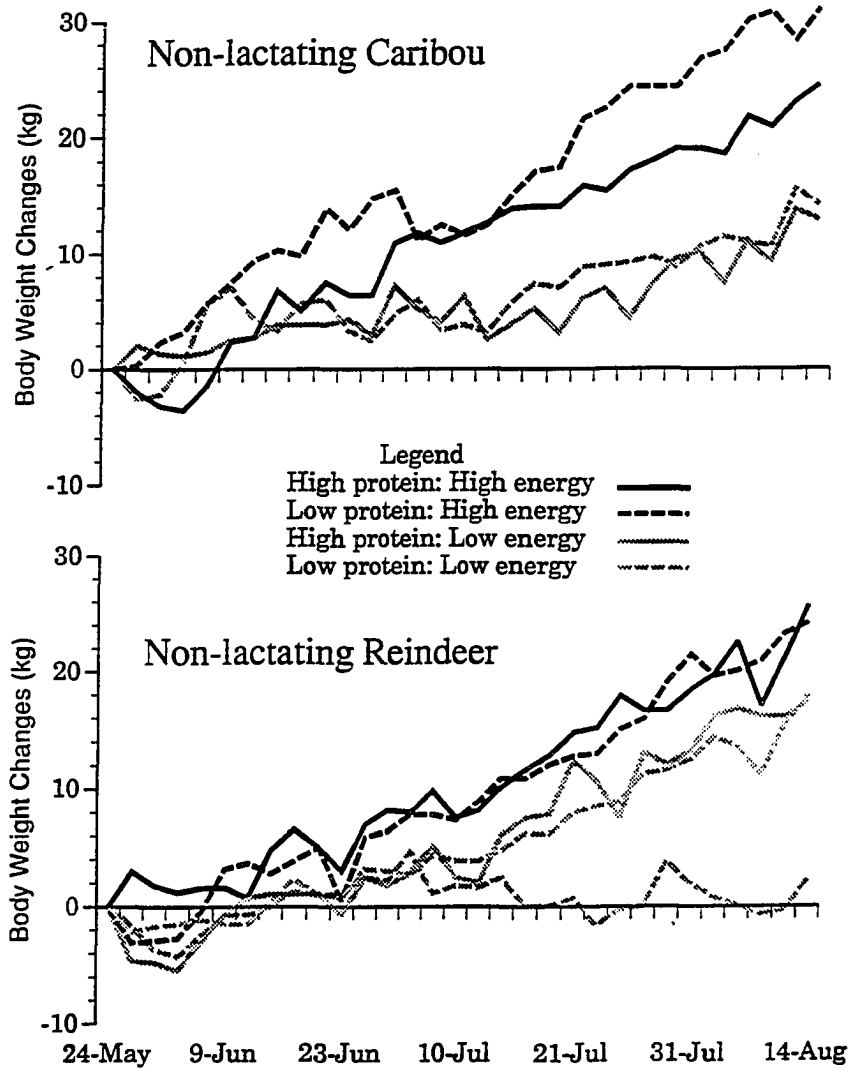

Figure 10. Body weight changes (kg) in individual non-lactating caribou and reindeer over the experimental period. The fifth non-lactating reindeer added as a reserve is also shown (net change on 14-Aug = 2.2 kg).

Body Fat

Among lactating caribou, mean body fat oscillated between 2.0 and 3.4% for 7 weeks before increasing sharply after July 10 (Figure 11). Mean fat composition in lactating reindeer initially exceeded that in lactating caribou by more than 7%, but declined markedly in early July when hot weather depressed appetite drive. Subsequently, mean fat composition in lactating reindeer approximated that in lactating caribou, and exhibited the same steep ascent after July 10.

Non-lactating females began and concluded the experimental period with higher fat compositions than their lactating counterparts, but followed a similar pattern of seasonal change (Figure 11). Among non-lactating caribou, mean body fat oscillated between 5.2 and 9.9% before climbing sharply after July 10. Non-lactating reindeer entered the experimental period with higher fat compositions than non-lactating caribou, but closely paralleled the other subspecies after June 19.

Because caribou entered the experiment leaner than reindeer but finished at a similar fat composition, they averaged a higher net gain in adipose tissue over the experimental period (Table 8). The maximum net adipose gain by any individual equalled 21.5 kg and occurred in a non-lactating caribou. The maximum net loss by any individual equalled 2.5 kg and occurred in a lactating reindeer.

Body Protein and Lean Tissue

In contrast to percent body fat, percent body protein was relatively stable throughout the experimental period (Figure 12). Body protein composition was also comparable between the 2 subspecies except at the beginning of the experiment when

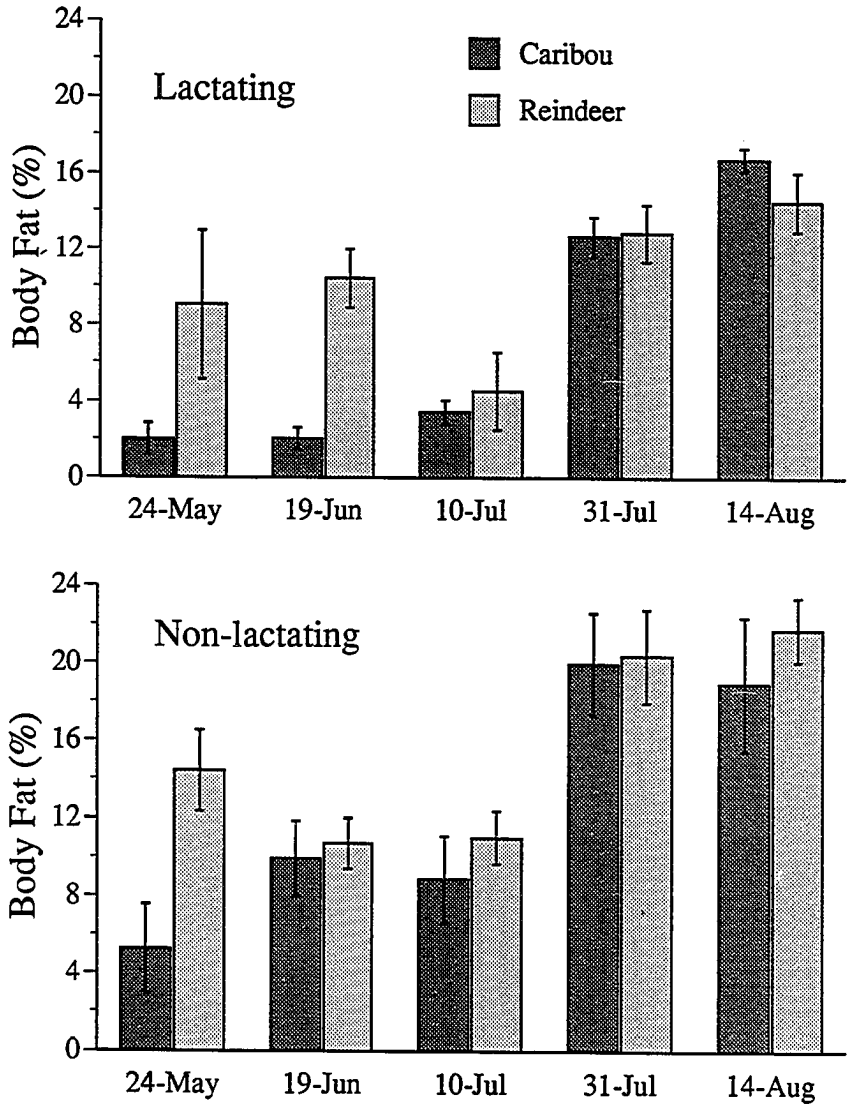

Figure 11. Body fat composition (%) of caribou and reindeer over the experimental period.

Table 8. Net change in adipose and lean tissue of experimental animals following a 12 week feeding trial.

	Mean	Minimum	Maximum	Std Error
Lactating Caribou				
Adipose Tissue (kg)	13.2	11.0	14.5	0.8
Lean Tissue (kg)	-2.0	-7.5	6.0	2.8
Lactating Reindeer				
Adipose Tissue (kg)	4.4	-2.5	9.6	2.5
Lean Tissue (kg)	1.9	-10.0	13.0	5.7
Non-lactating Caribou				
Adipose Tissue (kg)	12.1	6.8	21.5	3.5
Lean Tissue (kg)	4.1	3.0	6.0	0.7
Non-lactating Reindeer				
Adipose Tissue (kg)	8.1	5.0	13.3	1.8
Lean Tissue (kg)	5.4	-3.0	8.5	2.2

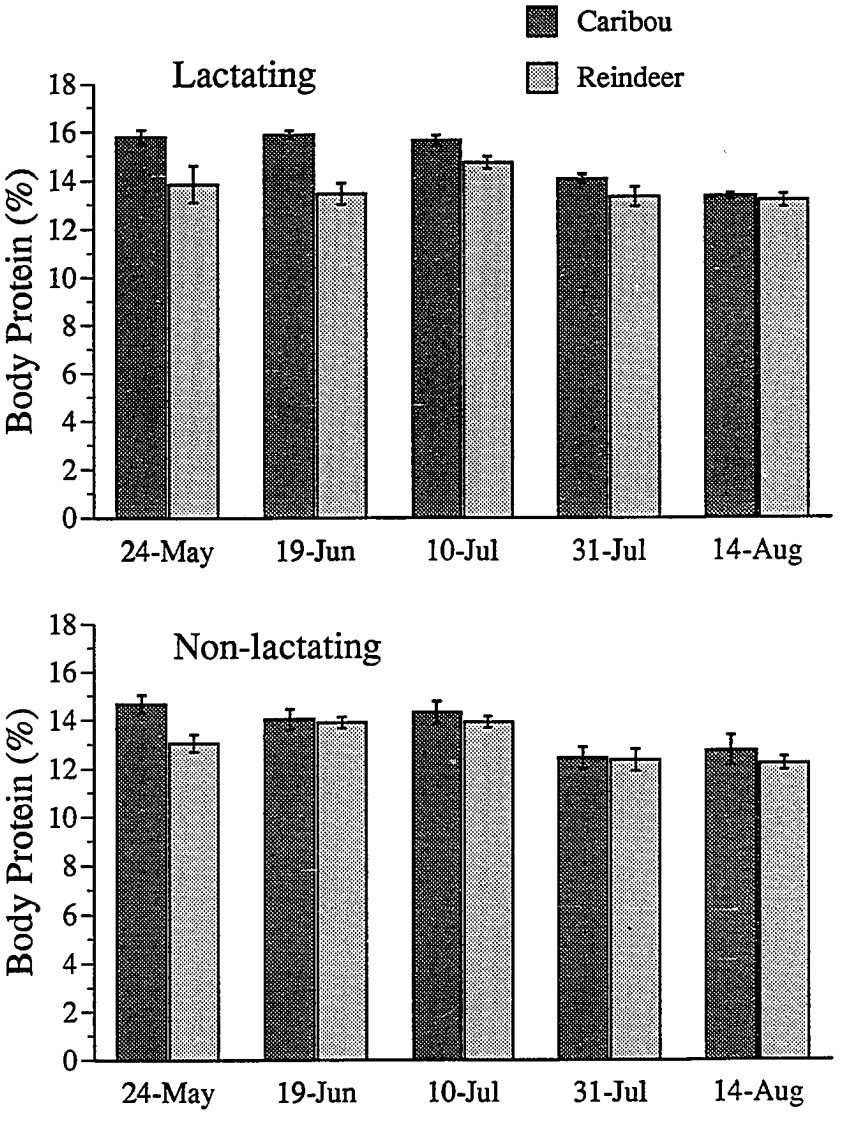

Figure 12. Body protein composition (%) of caribou and reindeer over the experimental period.

percent body protein was significantly higher in caribou than in reindeer. In both subspecies, protein composition declined by 1-2 percentage points towards the end of the 12 week experiment.

Final net gain in lean tissue was less than final net gain in adipose tissue for both subspecies and lactation classes (Table 8). The greatest disparity between fat and lean tissue deposition occurred in lactating caribou, which averaged a net gain of 13.2 kg fat but a net loss of 2.0 kg lean tissue after 12 weeks. Among the other 3 cohorts, net gain in lean tissue as a percentage of net adipose gain equalled 43.2% in lactating reindeer, 33.9% in non-lactating caribou, and 66.7% in non-lactating reindeer.

Milk

Milk water production, as measured by milk water intake, declined significantly ($p=0.0159$) throughout the experimental period for both caribou and reindeer (Figure 13). This decline was countered by a significant increase in milk dry matter ($p=0.0289$) when this parameter was measured between 61 and 112 days post-partum (Figure 14). Parallel increases in fat ($p=0.0044$) and energy ($p=0.0009$) contents were also observed during this period (Figure 14), but lactose concentration declined significantly ($p=0.0273$) while crude protein concentration remained unchanged. Neither milk nutrient composition (% wet weight) nor milk energy content (KJ/g wet weight) differed significantly between subspecies.

Lactose was the only milk parameter to negatively correlate with number of days post-partum ($p=0.0128$), despite declining trends in daily intake of milk dry matter, milk fat, milk protein, and milk energy (Figure 15). However, pairwise comparisons for individual calves revealed significant declines in daily intake of milk dry matter

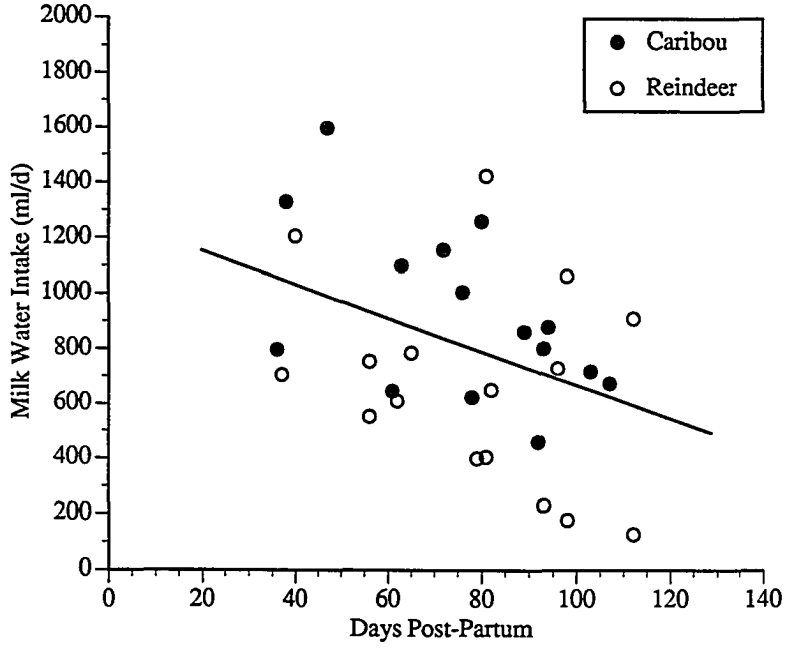

Figure 13. Daily milk water intake for caribou and reindeer calves.

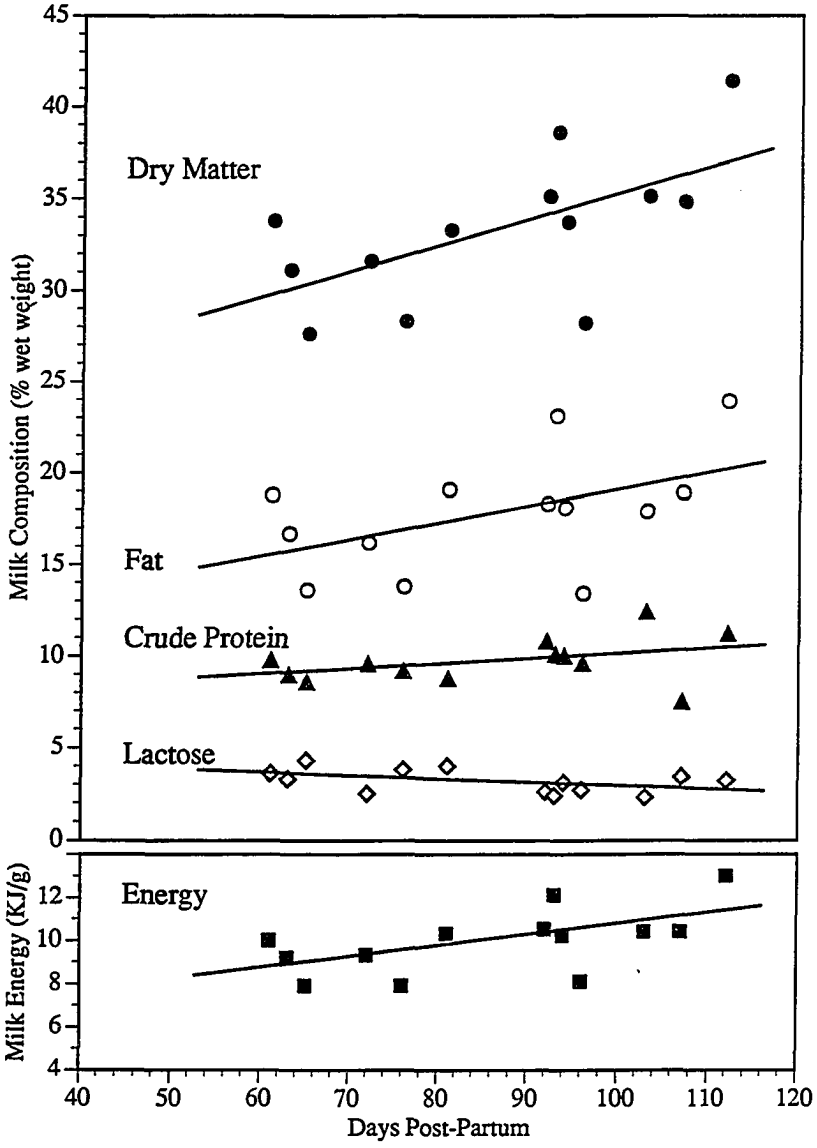

Figure 14. Dry matter, nutrient, and energy content of caribou and reindeer milk.

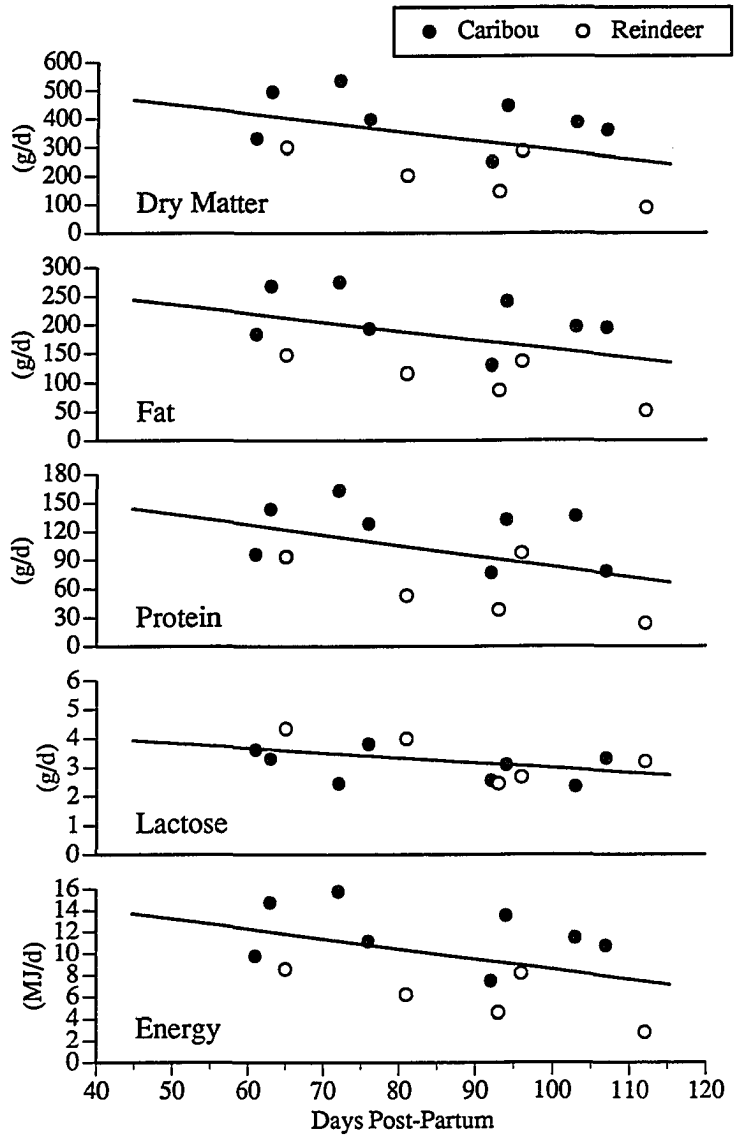

Figure 15. Daily milk nutrient and energy intake for caribou and reindeer calves.

($p<0.0159$), milk fat ($p<0.0305$), and milk protein ($p<0.0317$) between the 6th and 12th weeks of the experiment.

Effects of Nutrition, Season, and Body Condition

Body Weight

Energy intake (KJ/metabolic body weight) was the only independent variable significantly affecting body weight changes in either lactating or non-lactating females (Table 9). There was no subspecies effect. Regression slopes relating weight gain to energy intake were identical for the two cohorts and indicate the same efficiency for energy retention (Figure 16). However, the x-intercept was higher for lactating than non-lactating females at 456 and 233 KJ/metabolic body weight/day respectively (Figure 16). Daily net energy requirement for lactating females was therefore twice as high as for non-lactating females.

Body Fat

Fat deposition in both lactating and non-lactating females was significantly affected by time interval and starting fat composition (Table 9). The propensity for fat deposition increased with time but decreased with increasing fatness. Fat deposition in non-lactating females was additionally affected by energy intake, which promoted lipogenesis (Table 9). There was no subspecies effect.

Among lactating females, the effects of body condition were 1.8 times stronger than the effects of time interval, accounting for 41.3 and 22.8% of observed variations

Table 9. Partial r-squares, model r-squares, and p-values for independent variables significantly affecting weight gain and tissue deposition in lactating and non-lactating caribou/reindeer.

	LACTATING			NON-LACTATING		
	partial r^2	model r^2	p	partial r^2	model r^2	p
BODY WEIGHT CHANGES (kg)						
Net energy intake ($KJ/BW^{0.75}$)	0.5688	0.5688	0.0001	0.4959	0.4959	0.0001
BODY FAT DEPOSITION (kg)						
Net energy intake ($KJ/BW^{0.75}$)				0.1423	0.1423	0.0233
Body condition (% fat)	0.4131	0.4131	0.0001	0.2030	0.3454	0.0030
Time interval	0.2285	0.6416	0.0057	0.1470	0.4924	0.0046
BODY PROTEIN DEPOSITION (kg)						
Net energy intake ($KJ/BW^{0.75}$)	0.1228	0.1228	0.0307			
Body condition (% fat)	0.1874	0.3102	0.0133	0.3223	0.3223	0.0003
Time interval	0.2240	0.5341	0.0010	0.1631	0.4854	0.0028

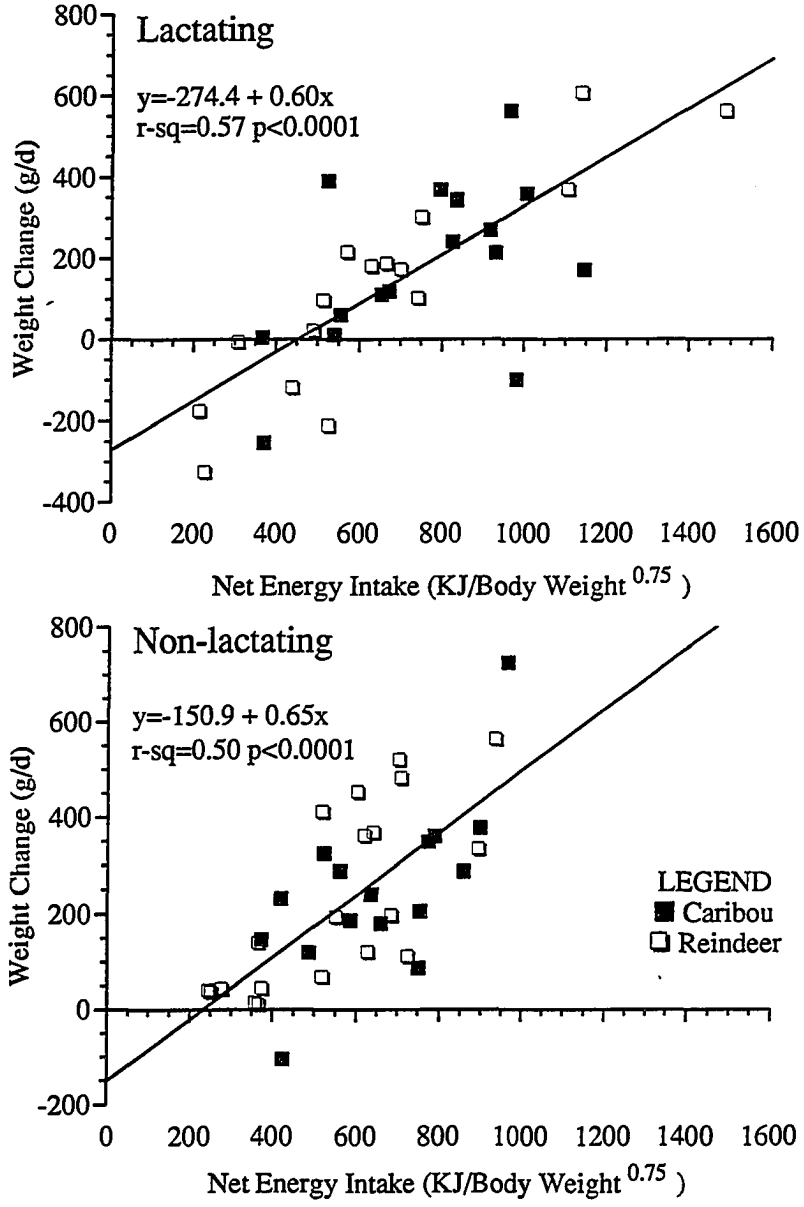

Figure 16. Relationship between body weight change and daily net energy intake in lactating and non-lactating caribou and reindeer.

in fat deposition respectively (Table 9). Among non-lactating females, body condition had the most dominant effect with a partial r-square of 0.20 (Table 9). Time interval and energy intake exerted secondary effects with partial r-squares of 0.15 and 0.14 respectively.

Body-Protein

Time interval and starting fat composition significantly affected protein deposition in both lactating and non-lactating females, but with effects opposite to those for fat deposition. Consequently, the propensity for protein deposition decreased with time but increased with increasing fatness. The effect of time outweighed the effect of body condition in lactating females, but the reverse was true in non-lactating females (Table 9). Among lactating females, energy intake exerted a positive, tertiary effect on protein deposition. There was no subspecies effect.

Milk

Milk water production increased significantly with maternal energy intake ($p<0.0001$) and decreased significantly with time ($p<0.0159$). The effects of energy intake were 76% greater than the effects of time, and together accounted for 59% of the observed variation in milk water volume.

Maternal nutrition did not affect daily production of milk dry matter, milk fat, or milk energy in caribou or reindeer. However, daily production of milk protein positively correlated with the maternal dietary protein:energy ratio ($p<0.0426$), while daily production of milk lactose positively correlated with maternal energy intake

($p<0.0001$). With the exception of milk lactose, daily milk nutrient and energy productions were significantly higher for caribou than reindeer.

Maternal nutrition also did not affect partitioning between maternal tissue deposition and production of milk dry matter, milk fat, or milk energy. However, milk protein production increased relative to maternal tissue deposition when the maternal dietary protein:energy ratio increased ($p<0.04$). Additionally, milk lactose production increased relative to maternal tissue deposition as maternal energy intake increased ($p<0.0001$), and decreased as time progressed ($p<0.01$).

Discussion

Fat and protein deposition in caribou and reindeer were strongly influenced by energy intake, date, and body condition, but were not affected by subspecies, protein intake, or the dietary protein:energy ratio. Weight gains in both lactating and non-lactating females were significantly affected by only energy intake. Date and body condition did not affect weight gain because their effects on fat deposition opposed and nullified their effects on protein deposition.

The regression between weight gain and energy intake (Figure 16) did not deviate significantly from linearity despite the established curvilinearity between energy balance and metabolic energy intake in domestic animals (Brody 1945, Blaxter and Boyne 1970). A lack of curvilinearity in these data is probably attributable to the limited range in energy intake, and to the scarcity of data points below maintenance. Furthermore, a lack of curvilinearity may be explained by compensatory changes in body composition underlying changes in body weight (Robbins 1983). A curvilinear relationship notwithstanding, the slope of the linear regression is used to estimate the efficiency of energy utilization (Van Soest 1982, Robbins 1983), and this slope did not differ between lactating and non-lactating females in this study. This contrasts with earlier work indicating a higher efficiency of weight gain (Moe et al. 1970) and fat deposition (Armstrong and Blaxter 1965) in lactating than non-lactating cows.

The daily net energy requirement of 456 $KJ/BW^{0.75}$ observed for lactating females in this study is 18% lower than that computed by Boertje (1985) for free-ranging caribou during the post-calving season when I assume a 60% net energy coefficient for fattening (Moe et al. 1970, ARC 1980 see p84). The daily net energy requirement of 233 $KJ/BW^{0.75}$ observed for non-lactating females in this study is

likewise 18% lower than that calculated by Holleman et al. (1979) for free-ranging caribou in winter. Lower maintenance requirements in this study are probably attributable to lower activity costs in penned animals. Boertje (1985) found a similar discrepancy of 20% when he compared his computed energetic requirements for free-ranging caribou in late winter with those measured for penned caribou and reindeer over the same season (McEwan 1970, McEwan and Whitehead 1970).

The positive correlation between fat deposition and energy intake in the non-lactating females concurs with earlier observations on steers (Purchas and Davies 1974, Berg and Butterfield 1976, Davies 1977, Byers 1982, Byers and Schelling 1988), wether lambs (Soeparno and Davies 1987a), white-tailed deer fawns (Holter and Hayes 1977, Holter et al. 1979), and immature caribou and reindeer (McEwan and Whitehead 1970). Such a relationship has been ascribed to a partitioning strategy that favors maintenance requirements and protein deposition over lipogenesis (Berg and Butterfield 1976, Byers 1982). However, as surplus energy increases with increasing intake, the proportion of total energy that is deposited as fat also increases. High energy diets can also result in significantly fatter animals because the associated increase in propionic acid concentration may stimulate lipogenesis by enhancing glucogenic activity (Soeparno and Davies 1987a, Van der Walt and Linington 1989). In high concentrate diets, passage of starch into the small intestines stimulates insulin production and further promote lipogenesis (Prior and Scott 1980). In contrast, fatty acid synthesis may be suppressed by a poor quality diet that increases acetic acid concentration but decreases the supply of glucogenic precursors (Van der Walt and Linington 1989).

Fat deposition in relation to energy intake has not been previously studied in lactating animals. However, results from this study demonstrated that lactating

females differ in their response from juveniles, males, and non-breeding females. In contrast to these cohorts, lactating females did not increase fat deposition with increased energy intake, probably because lactational expenditures imposed an energy limitation on maintenance metabolism and body protein deposition. Consequently, increases in energy availability were directed towards these functions, which are of higher priority than fat deposition (Berg and Butterfield 1976, Byers 1982). An energy limitation in lactating females is supported by the positive correlation between body protein deposition and energy intake in this cohort. In contrast, there was a notable absence of such a relationship in non-lactating females.

In this study, body fat and protein deposition were not affected by either protein intake or the dietary protein:energy ratio, but results from earlier studies have been mixed. Increased protein intake reportedly depressed fat deposition in calves (Donnelly and Hutton 1976) and white-tailed deer fawns (Holter and Hayes 1977, Holter et al. 1979), but had no apparent effect on cattle (Griffiths 1978, Lindsay and Davies 1981). Carcass fat composition in lambs was depressed by increased protein intake in studies by Norton et al. (1970) and Orskov et al. (1976), but was unchanged in studies by Craddock et al. (1974) and Soeparno and Davies (1987b). Moreover, carcass fat composition in goats increased with increasing dietary levels of rumen undegradable protein (Al Jassim et al. 1991).

Conflicting results between this study and those reporting significant protein effects may be partially explained by age differences in the experimental animals. Young animals are expected to respond more positively to increases in protein availability because they have a higher priority for muscle growth than older animals (Berg and Butterfield 1976, Byers and Schelling 1988). Studies that have shown a positive correlation between protein deposition and protein intake, but a negative

correlation between fat deposition and protein intake (Donnelly and Hutton 1976, Holter and Hayes 1977, Holter et al. 1979, Norton et al. 1970, Orskov et al. 1976), have been exclusively with immature animals, in contrast to this study which involved mature females.

The lack of a protein effect may also reflect the possibility that even animals on the lower protein diets were realizing the biological limit to protein deposition (Byers 1982). Excessive protein intake fails to improve protein retention in dairy cows and merely increases urinary loss of nitrogen (Kirchgebner et al. 1987). In some instances, protein synthesis may be limited by specific amino acids (MacRae and Lobley 1986) that are not appreciably increased by increased intake of a diet unchanged in composition. Lower protein intakes are also compensated by an increased efficiency of nitrogen recycling (Van Soest 1982) that is further promoted by the high salivary volume associated with poorer quality diets (Egan et al. 1986). Increased nitrogen recycling also increases protein retention by shifting dependency on urea nitrogen, which allows a higher utilization efficiency than protein source nitrogen (Cock et al. 1967).

Protein synthesis may also be limited by energy supply, which can exert an even greater effect on nitrogen balance than protein supply (Syrjala et al. 1980, Syrjala-Qvist and Salonen 1983, MacRae and Lobley 1986). Strong correlations between nitrogen balance and the molar concentrations of volatile fatty acids (McRae and Lobley 1976) are similarly attibutable to the higher effective energy of propionic than acetic acid (McRae and Lobley 1976, Soeparno and Davies 1987b).

Such interactions between protein and energy have prompted Van der Walt and Linington (1989) to conclude that there is an optimal protein:energy ratio for maximum utilization efficiency of both dietary protein and energy. Similarly,

Soeparno and Davies (1987b) noted that when protein absorption is markedly in excess of requirements for protein synthesis, the concommitant increase in heat production may actually result in less energy available for lipogenesis. Such relationships would readily explain the inhibitory effect of high protein intake on fat deposition reported by some authors (Donnelly and Hutton 1976, Holter and Hayes 1977, Holter et al. 1979, Norton et al. 1970, Orskov et al. 1976). However, the lack of a similar effect in this and other studies (Craddock et al. 1974, Griffiths 1978, Lindsay and Davies 1981, Soeparno and Davies 1987b) can be explained by energy released from deamination of the excess protein. Thus, as protein intake increased beyond requirements for protein synthesis, resultant declines in utilization efficiencies may well have been counteracted by surplus energy made available from amino acid degradation.

Protein intake may also have failed to affect body reserve deposition in this study because dietary protein was also being used for pelage production during the experimental period. Although hair growth was not quantified, pelage development in high intake animals was clearly more advanced than in animals with low appetite drive. By the end of the 12 week experiment, 2 particularly thin individuals had still not completely shed the previous winter pelage, in sharp contrast to others that had one cm or more of new hair growth. Pelage production was therefore a major nitrogen sink that could have obscured differential intakes in dietary protein.

The increasing propensity for lipogenesis between spring and fall was shown to be independent of nutritional intake, and extends previous findings on white-tailed deer fawns (Abbot et al. 1984), isolated reindeer adipocytes (Larsen et al. 1985), and free-ranging caribou (Chapter 1). This seasonal shift in nutrient partitioning is ostensibly under photoperiodic regulation, with lipogenesis being increasingly

stimulated by the shortening fall photoperiod (Abbot et al. 1984). Despite the preferential deposition of body fat in fall, the importance of summer lipogenesis is underscored by impressive adipose gains over the experimental period that reached 14 and 21 kg in a lactating and non-lactating caribou respectively. In free-ranging caribou, absolute fat deposition in summer (12 g/d for lactating females; 53 g/d for non-lactating females) greatly exceeded that in fall (6 g/d for lactating females; -64 to 39 g/d for non-lactating females) even though lipogenesis was of diminished priority in summer (Chapter 1).

Milk composition found in this study approximated trends and values documented for pasture-grazing reindeer (Luick et al. 1974) and penned caribou fed pelleted ration and chopped brome hay (Parker et al. 1990). In these studies, milk dry matter (Luick et al. 1974, Parker et al. 1990), milk fat (Luick et al. 1974) and milk energy (Parker et al. 1990) similarly increased following 60 days post-partum, while milk lactose declined (Luick et al. 1974) and milk crude protein remained relatively unchanged (Parker et al. 1990). Similarities in milk compositions among the variably fed caribou and reindeer of these 3 studies support White and Luick's (1984) observation of relative inelasticity in *Rangifer* milk composition.

In this study, declining milk volumes associated with either time or undernutrition were largely compensated by increases in milk quality. These results concur with previous evidence from Loudon and Kay (1984) indicating that the principal correlate of milk energy content for red deer may be yield rather than lactation stage per se. Working with reindeer, White and Luick (1984) additionally demonstrated negative correlations between milk volume and compositions of fat, protein, and energy. The results also agree with those of Parker et al. (1990), who found little change in milk protein and energy consumption in caribou calves between

60 and 100 days of age. However, elevated protein and energy intakes were more apparent between birth and 30 days post-partum (Parker et al. 1990).

The independence of milk fat and energy output to either calf age or maternal nutrition underscores the cow's commitment to milk production, and does not support a shifting priority from lactation as the calf ages. However, milk composition data were only available between 60 and 100 days post-partum, and this conclusion may not necessarily apply to the entire lactation cycle. Furthermore, in concurrence with White and Luick (1984), the results do support an earlier weaning date in nutritionally restricted females. Milk water volume decreased significantly with reduced energy intake and milk concentration approximated that of late stage lactation.

Lactating females suffering negative energy balance are physiologically predisposed towards fulfilling lactational demands at the expense of adipose reserves. Larsen et al. (1983) demonstrated that lipolysis in isolated reindeer adipocytes is inhibited by acetic and propionic acids. Conversely, glucose and propionic acid promote the release of insulin, which is ineffective in the ruminant mammary but promotes lipogenesis in maternal adipose tissue (Rook and Thomas 1983). Maternal lipolysis is therefore suppressed and tissue deposition promoted in high intake animals, especially when fed concentrate diets that promote ruminal propionic acid production and subsequent insulin release. In contrast, lipolysis proceeds freely in low intake animals on poor quality diets, and mobilized substrates are channeled towards milk production. Moreover, nutritionally stressed females may preferentially use body reserves to drive lactation since the net energy coefficient for milk secretion is significantly higher for body energy (0.84) than for metabolizable energy (0.52-0.72) (ARC 1980).

Lactional output in undernourished females is additionally induced by persistent nursing attempts from calves unreconciled to low milk volumes. Espmark (1980) found that undernourished cows showed a higher frequency of maternal rejection, shorter nursing bouts, and reduced maternal licking; however, nursing frequency was increased. A similar increase in nursing frequency has been reported for red deer grazing poor hill pasture when compared with dams on high quality rye grass-clover swards (Loudon and Kay 1984). Such an increased frequency of mammary voiding interrupts the autocrine feedback modulation in which chemical inhibitors in the milk suppress further secretion by the mammary (Peaker and Wilde 1987).

The proclivity of lactating females to sacrifice body fat for milk production contrasts with their relative disinclination for doing the same with body protein. In contrast to milk fat and milk energy output, milk protein output was significantly reduced by a low dietary protein:energy ratio. Since maternal protein deposition may be energy limited as previously discussed, these results suggest that lactating females may direct only surplus protein not utilized for maternal tissue towards milk production. Such a suggestion would be consistent with the positive correlation between maternal energy intake and maternal protein deposition found in this study. A leading priority for protein repletion over the summer is compatible with the energy rich but protein poor lichen-dominated diets characterizing fall and winter (Russell and Martell 1984, Martell et al. 1986, Thomas and Hervieux 1986, Thomas and Barry 1990, Russell and Martell unpub. data). Failure to deposit body protein over the summer is therefore especially critical given the preclusion of subsequent opportunities.

Milk lactose production was unique both because it declined significantly over time and also because it increased significantly with increased maternal energy intake. The positive correlation between lactose production and maternal energy intake is clearly mediated through plasma glucose, which supplies 64-100% of the carbon for milk lactose synthesis (Luick et al. 1983). Glucose production, in turn, has been shown to increase with increased energy intake (McEwan et al. 1976). The decline in milk lactose production over time coincides with seasonal declines in both glucose transfer rate and irreversible loss (White and Luick 1976). This declining production may be consistent with a strategy that encumbers less than 18% glucose irreversible loss for milk lactose even at peak lactation (White and Luick 1984). White and Luick (1984) proposed this to be a conservation measure that maximizes the glucose carbon available for more critical functions of the dam. Alternatively, low lactose concentrations permit a concentrated milk (Linzell and Peaker 1971, Peaker 1977) that minimizes nursing time and hence, reduce the potential of predation (White and Luick 1984, Loudon and Kay 1984).

In summary, the study results supported the hypotheses of increased lipogenesis with increased energy intake (Ho_{1a}), time (Ho_{1d}) and leanness (Ho_{1e}). In rejection of Ho_{1b} and Ho_{1c}, neither protein intake nor the dietary protein:energy ratio had any effect on body tissue deposition. Among lactating females, nutrient partitioning between maternal tissue deposition and milk production varied with milk nutrient. In rejection of Ho_2, production of milk dry matter, milk fat, and milk energy were unaffected by time interval, maternal energy intake, maternal protein intake, or maternal body condition . However, in acceptance of Ho_{2a} and Ho_{2c}, milk lactose production positively correlated with maternal energy intake, while milk protein

production positively correlated with the maternal dietary protein:energy ratio. Only milk water production and lactose output changed significantly with calf age (Ho_{2d}).

Chapter 3.
Adipose Dynamics and the Prediction of Body Weight and Body Composition in Femaie Barren-ground Caribou

Introduction

Body weight and body composition are important determinants of population growth potential in caribou and reindeer, affecting ovulation and conception rates (Dauphiné 1976, Klein and White 1978, Thomas 1982, Reimers 1983, Cameron et al. 1990), age of first reproduction (Leader-Williams and Rosser 1983), and survival (Thomas et al. 1976, Haukioja and Salovaara 1978). Routine monitoring of body weight and composition is consequently important for assessing changes in demographic vigor. Frequently, disturbances arising from industrial development or insect and predator harassment are manifested not in direct mortality but in more subtle changes in body weight and composition (Klein 1991). Additionally, population displacement to inferior habitat or range degradation resulting from overpopulation are likewise reflected in depressed weights and body reserves (Klein 1968, Reimers 1983, Skogland 1983, 1984).

The need to monitor body weight and composition is especially pressing for barren-ground caribou (*Rangifer tarandus granti*) of the Porcupine Herd (Porcupine Caribou Management Board 1989, 1990). Firstly, proposed petroleum exploration and development along the arctic foothills and coastal plains of the Beaufort Sea threaten to interfere with the calving and post-calving activities of the herd (Whitten and Fancy 1990, Young et al. 1990, Klein 1991). Additionally, steady population

expansion from 110,000 animals in 1979 (Garner and Reynolds 1986) to a current population of 178,000 (Fancy et al. 1990) has significantly altered the population density. Management prescriptions are frustrated by the uncertainty of whether the population is approaching, at, or exceeding its range carrying capacity , and there is concern that an unsustainable density may lead to a population crash. This problem is not unique to the Porcupine Herd; in fact, the increasing status of the world's largest *Rangifer* populations (Williams and Heard 1986) render this a global predicament.

Indicator bone, muscle, and fat measurements of shot animals have been used successfully by several investigators to project body weights and composition in *Rangifer* (Dauphiné 1971, Ringberg et al. 1981, Huot and Groudreault 1985, Adamczewski et al. 1987). These indices are particularly fitting for populations such as the Porcupine Herd where a single access road to a major wintering site facilitates the use of check stations to obtain data from hunter-killed animals. Under this system, a large number of samples can be collected at low cost and labor. Conversely, animals may be shot specifically for monitoring purposes, but minimal work is needed to measure indices and predict total body composition once the animals have been killed.

Unfortunately, the application of this technique is hampered by the inappropriateness of existing indices for projecting body weight and composition in migratory caribou. Previous work had focused on reindeer (Ringberg et al. 1981) and non-migratory caribou (Adamczewski et al. 1987), and allometric relationships for these subspecies likely differ from those of the long-legged and highly mobile barren-ground caribou. Dauphiné (1971) addressed allometric relationships in migratory caribou but did not investigate total body composition. Huot and Goudreault (1985) presented useful equations for projecting body fat, but restricted equations to the use of single indices. Predictions of body weight and protein reserves were not addressed.

In the above studies, many selected indices are also difficult to obtain from hunter-killed animals.

The objective of this study was to develop prediction equations of body weight and composition for female barren-ground caribou using bone, muscle, organ, and fat indices that can be easily and accurately measured in a monitoring program. I evaluate 38 continuous parameters for their predictability of body weight, combined carcass and viscera weight, body fat, and body protein.

Methods

The Porcupine Herd has a distributional range of 250,000 km^2 (64-70°N, 130-150°W) covering northeastern Alaska, northern Yukon Territory, and the western border of Northwest Territories. Female caribou were collected from this population four times annually in both 1987 and 1988, in March-April, June, September, and November. Collections followed seasonal migrations from the coastal plains of the Beaufort Sea in June, to the Old Crow Flats in September, and south to the wintering ranges at either Eagle Plains, Y.T., or Arctic Village, AK., in November and March-April. Five to twelve females were taken at each collection for a total sample of 68. Only females older than 24 months were included in the analyses.

Harvested animals were immediately weighed and measured for body length, chest girth, forefoot length, and hindfoot length (Langvatn 1977). The animal was skinned and the skull removed at the atlas. Visceral organs were individually separated and weighed. Kidneys were excised perpendicular to the longitudinal axis at either end and weighed with and without the surrounding fat. The perirenal fat was not trimmed but was removed intact with the tunica fibrosa. The kidney fat index was calculated as the weight of untrimmed fat divided by kidney weight. The digestive tract was cleaned of contents and the tissue combined with the other viscera.

The eviscerated carcass was bisected longitudinally through the vertebrae and the right half was analysed for chemical composition. Indicator bones (femur, tibia-fibula, and metatarsus) and indicator muscles (*Muscle gastrocnemius*, and *M. peroneus tertius* with *M. extensor digitorum longus* and *M. extensor digit III* attached) were dissected from the left half carcass and weighed. Indicator muscles were also analysed for chemical composition. Indicator bones were frozen prior to marrow

extraction to prevent oil loss. Extracted marrows were weighed and freeze-dried. Percent marrow fat was estimated using regression equations by Neiland (1970), then multiplied by marrow weight to give marrow fat weight. Depth of back fat, lower jaw length, and indicator bone lengths were measured according to Langvatn (1977). Aging was done by counting tooth cementum annuli (Matson's Laboratory, MT; McEwan 1963, Reimers and Nordby 1968, Miller 1974).

Sawdust homogenates of the half carcass and viscera were produced by sectioning at approximately 1 cm intervals using a Hobart bandsaw (Huot and Picard 1988). Indicator muscles were ground twice in a meat grinder fitted with a 3 mm mesh sieve. Homogenates of the half carcass, viscera, and indicator muscles were then separately analysed for fat content using the methanol-chloroform technique (Christie 1982). Water content was determined by freeze-drying homogenate samples for 72 hours. Samples already extracted for fat and water (i.e. fat-free dry matter) were then determined for crude protein content using kjeldahl analysis and a specific factor of 6.25 (AOAC 1984). All analyses were done in 2-4 replicate samples. A ratio of wet to dry crude protein was computed on the premise that all water content is in the lean tissue. Separate ratios were computed for skeletal and smooth muscle, then weighted for the skeletal and smooth muscle compositions of female caribou to produce a single multiplier for converting body dry crude protein to body wet crude protein. Water content for skeletal muscles was estimated from the peroneus tertius. Water content for smooth muscles was estimated from the combined viscera.

Body weight in this study refers to animal weight immediately after death, while combined carcass and viscera (carcass+viscera) weight refers to body weight minus the weights of skull, antlers, hide, and gastrointestinal contents. Total body

composition was computed from the weighted compositions of the carcass and viscera, and therefore excludes compositions of the skull, antlers, and hide.

Stepwise multiple regression (SAS Institute Inc. 1985) was used to develop predictive equations for body weight and body composition from a selection of 38 continuous independent variables (Table 10). Season and reproductive status were also included as categorical variables. Only independent variables significant at $p < 0.05$ were entered into the regression model. Independent variables were individually checked for linearity with the dependent variable and straightened by transformation if nonlinear. Percentage variables were arcsine transformed in radians (Zar 1984). Saturation functions, in which the dependent and independent variables become decoupled at high values, were transformed with the normal score (Conover 1980). Interactive terms were included in the selection list to allow for potential interactions between independent variables. Missing values due to field damage reduced the sample size of various independent variables (Table 10). Consequently, regression analysis was repeated a second time using only independent variables selected in the initial stepwise procedure in order to maximize sample size for the final equation.

Model aptness was evaluated by examining residuals and studentized deleted residuals (Neter et al. 1985). Multicollinearity among independent variables was circumvented by excluding models with a variance inflation factor > 10 (Neter et al. 1985) or those containing variable pairs with an absolute correlation coefficient > 0.69 (Bowyer et al. 1988). The Durbin-Watson test was used to check for autocorrelation.

Prediction equations of body weight were further validated by testing with an independent data set (Smits et al., unpub. data) collected from the same population. Sampling periods for the independent data set corresponded with seasonal collections for this study, and occurred in September 1989, November 1989, March 1990, and

Table 10. Means, standard deviations, and ranges of continuous independent variables evaluated for the prediction of body weight and body composition in female caribou aged > 24 months.

VARIABLE	n	CODE	MEAN	SD	RANGE
Body length (cm)	63	BODLEN	177.1	11.7	121.5 - 196.0
Chest girth (cm)	64	CHEST	117.1	5.8	107.5 - 129.0
Forefoot length (cm)	64	FFOOT	39.8	1.5	36.5 - 43.0
Hindfoot length (cm)	64	HFOOT	54.1	1.5	51.0 - 59.1
Gastrocnemius wt (g)	64	GASTR	559.4	74.3	410.0 - 800.0
Gastrocnemius fat (%)	65	GASLIP	3.9	1.0	1.8 - 7.6
Gastrocnemius water (%)	65	GASH2O	74.4	1.3	71.0 - 77.1
Peroneus tertius wt (g)	65	PERTER	147.2	17.7	105.3 - 191.0
Peroneus tertius fat (%)	65	PERLIP	3.6	0.8	2.1 - 5.4
Peroneus water (%)	65	PERH2O	75.1	1.4	71.8 - 78.0
Femur wt (g)	64	FEMWT	367.6	32.7	289.9 - 435.6
Femur length (cm)	64	FEMLEN	28.3	0.8	26.6 - 29.9
Femur marrow fat (g)	64	FMFWT	38.1	10.4	8.3 - 58.9
Femur marrow fat (%)	65	FMF	69.4	19.7	4.0 - 88.7
Femur marrow water (%)	65	FMH2O	28.1	18.8	9.7 - 90.6
Tibia-fibula wt (g)	65	TIBIAWT	325.1	26.5	271.0 - 376.5
Tib-fib length (cm)	65	TIBIALEN	32.8	0.9	30.1 - 35.0
Tib-fib marrow fat (g)	65	TMFWT	49.2	10.1	25.8 - 73.2
Tib-fib marrow fat (%)	65	TMF	74.0	22.2	3.7 - 93.6
Tib-fib marrow water (%)	65	TMH2O	23.7	21.2	5.0 - 90.9
Metatarsus wt (g)	65	METAWT	224.8	17.7	180.3 - 259.5
Metatarsus length (cm)	65	METALEN	30.5	1.0	27.5 - 32.1
Meta. marrow fat (g)	65	MMFWT	33.1	8.3	11.2 - 53.1
Meta. marrow fat (%)	65	MMF	76.6	22.1	6.6 - 94.6
Meta. marrow water (%)	65	MMH2O	21.2	21.1	4.0 - 88.1
Back fat (cm)	65	BACKFAT	0.36	0.8	0 - 3.0
Heart (kg)	61	HEART	0.93	0.2	0.5 - 1.4
Liver (kg)	60	LIVER	1.23	0.3	0.6 - 2.1
Right kidney wt (g)	65	RKIDNEY	99.2	18.0	69.5 - 156.0
Right kidney fat (g)	65	RKIDFAT	29.5	16.6	6.7 - 76.4
RKIDFAT index (%)	65	RKFI	30.3	16.9	6.9 - 68.0
Left kidney weight (g)	65	LKIDNEY	101.0	18.6	65.4 - 170.0
Left kidney fat (g)	65	LKIDFAT	31.2	20.2	6.0 - 108.0
LKIDFAT index (%)	65	LKFI	31.9	20.9	5.5 - 106.9
Mean (Rkidfat,Lkidfat)	65	RLKIDFAT	30.4	18.0	6.3 - 85.0
Mean (RKFI,LKFI)	65	RLKFI	31.1	18.4	7.1 - 85.0
Lower jaw length (cm)	56	LJAW	27.6	0.9	24.7 - 29.2
Age (yr)	65	AGE	6.8	2.8	2.3 - 13.5

September 1990. Data collected included both body weight and indices of body weight described in this study. Data collections were collaboratively conducted by hunters and conservation officers trained with the assistance of a demonstration video, and comprise a population monitoring program for the Porcupine Herd (Porcupine Caribou Management Board 1989, 1990).

After a best model had been selected by stepwise multiple regression, independent variables that are difficult to obtain were systematically removed from the selection list, both singly and in combination with other difficult to obtain variables. Stepwise multiple regressions were then repeated with these incomplete variable lists. A series of alternative equations was therefore generated for situations where certain predictor variables may be lacking. Variables considered difficult to obtain from hunter-killed animals were based on questionnaires to wildlife agencies, and included measurements on the femur, which is difficult to access because of its buried position, and the gastrocnemius, which is a relatively large muscle not readily relinquished by the hunter. Variables requiring extensive laboratory analysis were also considered difficult to obtain, and include fat measurements from the gastrocnemius and the peroneus tertius. External dimensions that had to be measured before dressing were also systematically eliminated to permit data collection from hunter-killed animals.

Results

Body Weight

The best single predictors of body weight were, in descending order, heart weight, gastrocnemius weight, peroneus tertius weight, and liver weight (Table 11). Many of the other predictor variables also correlated significantly with body weight but individually accounted for less than 30% of the observed variation (Table 11). None of the continuous predictor variables deviated from a linear relationship with body weight, and neither age, season, nor reproductive status were significant factors in multiple regression analysis.

The multiple regression equation with the highest adjusted r-square (adj-r^2) consisted of 5 predictor variables including femur weight (Tables 3 and 4). Removal of femur weight from the selection list resulted in Equation 2 (Table 13) and a reduction in the adj-r^2 of only 0.01. Equations not requiring external dimensions are given by Equations 3 and 4 (Table 13), with 3 and 2 predictor variables respectively.

Testing with an independent data set revealed that all equations predicted within the 95% confidence interval of the observed mean for all four sample collections (Table 14). Equation 1 (Table 13), with the largest number of predictor variables and the highest adj-r^2, did not differ by more than 3.4 kg between observed and predicted mean for any collection period. The maximum difference between observed and predicted mean occurred with Equation 3 (Table 13) for September 1989. However, Equation 3 also showed the smallest difference between observed and predicted mean for November 1989 and March 1990, at -1.5 and 0.3 kg respectively (Table 14).

Table 11. Simple linear regressions for predicting body weight (y; kg) in female caribou aged > 24 months.

x	EQUATION	n	r^2	RMSE	p
CHEST	$y = 6.2 + 0.7192\,x$	64	0.17	9.2	0.0007
GASTR	$y = 42.3 + 0.0865\,x$	64	0.42	7.6	0.0001
PERTER	$y = 38.8 + 0.3542\,x$	65	0.40	7.8	0.0001
FEMWT	$y = 34.9 + 0.1523\,x$	64	0.25	8.8	0.0001
FEMLEN	$y = -62.8 + 5.4357\,x$	64	0.17	9.2	0.0007
TIBIAWT	$y = 33.7 + 0.1760\,x$	65	0.22	8.9	0.0001
TIBIALEN	$y = -46.2 + 4.1859\,x$	65	0.15	9.2	0.0014
BACKFAT	$y = 88.9 + 5.3876\,x$	65	0.19	9.0	0.0003
HEART	$y = 55.6 + 37.6176\,x$	61	0.47	7.3	0.0001
LIVER	$y = 65.6 + 21.0009\,x$	60	0.37	8.1	0.0001
RKIDNEY	$y = 66.0 + 0.2506\,x$	65	0.20	8.9	0.0002
RKIDFAT	$y = 83.1 + 0.2641\,x$	65	0.19	9.0	0.0002
LKIDNEY	$y = 66.5 + 0.2419\,x$	65	0.20	9.0	0.0002
LKIDFAT	$y = 83.1 + 0.2500\,x$	65	0.26	8.6	0.0001
AGE	$y = 80.9 + 1.4557\,x$	65	0.17	9.1	0.0007

Table 12. Comparison of indices in alternative equations (Table 13) for predicting body weight (kg), carcass+viscera weight (kg), body fat (%), and body dry crude protein (%).

Y:	Body Weight				Carc+Visc Weight					Body Fat					Body Protein			
Eqn:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
CHEST	x	x																
HFOOT					x	x									x	x		
GASTR				x														
GASLIP										x	x				x	x	x	
GASH2O														x				
PERTER					x	x	x	x										
FEMWT	x																	
FMF															x			
FMFWT											x							
FMH2O					x													
TIBIAWT			x						x								x	
TMF	x	x														x		
TMH2O										x		x		x				
METAWT								x										x
METALEN															x	x	x	x
MMFWT																		x
MMH2O													x					
BACKFAT					x	x	x											
HEART	x	x	x	x	x		x	x	x						x	x	x	
LIVER					x	x	x	x										
RKIDNEY	x	x																
LKIDNEY																		x
LKIDFAT			x					x	x			x	x					
RLKIDFAT										x	x							
SEASON										x	x	x						

Table 13. Multiple regression equations for predicting body weight (kg), carcass+viscera weight (kg), body fat (%), and body dry crude protein (%) in female caribou aged > 24 months. Sine and arcsine functions are in radians. Coding for season: 1 - June, 2 - September, 3 - November, and 4 - March. See Figures 17-19 for normal scores (Nscore) of marrow water.

	EQUATION	n	adj-r^2	RMSE*	p
Body Weight (kg)					
(1)	Y = -23.5 + 0.4056 CHEST + 25.5284 HEART + 0.0495 FEMURWT + 0.1484 RKIDNEY + 0.1275 TMF	59	0.719	5.31	0.0001
(2)	Y = -21.6 + 0.5040 CHEST + 25.7891 HEART + 0.1862 RKIDNEY + 0.1354 TMF	60	0.704	5.40	0.0001
(3)	Y = 16.0 + 27.0060 HEART + 0.1410 TIBIAWT + 0.1235 LKIDFAT	62	0.625	6.07	0.0001
(4)	Y = 35.0 + 0.0534 GASTR + 27.4213 HEART	61	0.620	6.07	0.0001
Carcass+Viscera Weight (kg)					
(5)	Y = -30.1 + 0.9233 HFOOT + 0.1411 PERTER + 5.6058 HEART + 6.5828 LIVER + 2.9876 BACKFAT - 0.8883 Nscore (FMH2O)	55	0.865	2.69	0.0001
(6)	Y = -33.4 + 0.9398 HFOOT + 0.1866 PERTER + 7.4381 LIVER + 3.3675 BACKFAT	59	0.846	2.86	0.0001
(7)	Y = 12.4 + 0.2037 PERTER + 5.2898 HEART + 5.4556 LIVER + 2.6668 BACKFAT	56	0.835	2.96	0.0001
(8)	Y = 3.4 + 0.1403 PERTER + 6.0857 HEART + 5.3783 LIVER + 0.0644 METAWT + 0.1352 LKIDFAT	56	0.847	2.85	0.0001
(9)	Y = 8.6 + 12.9237 HEART + 0.0855 TIBIAWT + 0.2070 LKIDFAT	61	0.762	3.49	0.0001

...cont'd.

Table 13 cont'd.

Body Fat (%)					
(10)	$Y = [\ \text{Sin}\ (0.18156 + 0.00112\ \text{RLKIDFAT} + 0.01561\ \text{GASLIP} - 0.01768\ \text{Nscore}\ (\text{TMH2O}) + 0.01109\ \text{SEASON})\ ]^2 \cdot 100$	61	0.833	0.0213	0.0001
(11)	$Y = [\ \text{Sin}\ (0.13356 + 0.00152\ \text{FMFWT} + 0.00102\ \text{RLKIDFAT} + 0.01900\ \text{GASLIP} + 0.00904\ \text{SEASON})\ ]^2 \cdot 100$	60	0.828	0.0218	0.0001
(12)	$Y = [\ \text{Sin}\ (0.23654 + 0.00124\ \text{LKIDFAT} - 0.02191\ \text{Nscore}\ (\text{TMH2O}) + 0.01190\ \text{SEASON})\ ]^2 \cdot 100$	61	0.778	0.0245	0.0001
(13)	$Y = [\ \text{Sin}\ (0.23286 - 0.02129\ \text{Nscore}\ (\text{MMH2O}) + 0.00118\ \text{LKIDFAT} + 0.01373\ \text{SEASON})\ ]^2 \cdot 100$	61	0.758	0.0256	0.0001
(14)	$Y = [\ \text{Sin}\ (1.66676 - 0.01832\ \text{GASH2O} - 0.02537\ \text{Nscore}\ (\text{TMH2O}))\ ]^2 \cdot 100$	61	0.734	0.0269	0.0001
Body Dry Crude Protein (%)					
(15)	$Y = [\ \text{Sin}\ (0.47203 - 0.00439\ \text{HFOOT} + 0.02741\ \text{HEART} + 0.00642\ \text{METALEN} - 0.01342\ \text{GASLIP} + 0.00051\ \text{FMF})\ ]^2 \cdot 100$	56	0.692	0.0119	0.0001
(16)	$Y = [\ \text{Sin}\ (0.48197 - 0.00459\ \text{HFOOT} + 0.03239\ \text{HEART} + 0.00641\ \text{METALEN} - 0.01287\ \text{GASLIP} + 0.00040\ \text{TMF})\ ]^2 \cdot 100$	56	0.665	0.0124	0.0001
(17)	$Y = [\ \text{Sin}\ (0.29653 + 0.04480\ \text{HEART} + 0.00626\ \text{METALEN} - 0.00017\ \text{TIBIAWT} - 0.00870\ \text{GASLIP})\ ]^2 \cdot 100$	57	0.470	0.0155	0.0001
(18)	$Y = [\ \text{Sin}\ (0.09170 - 0.00056\ \text{METAWT} + 0.01350\ \text{METALEN} + 0.00063\ \text{MMFWT} + 0.00047\ \text{LKIDNEY})\ ]^2 \cdot 100$	61	0.472	0.0152	0.0001

*RMSE units in kg for body and carcass+viscera weights, and in arcsine transformed units for body fat and body protein.

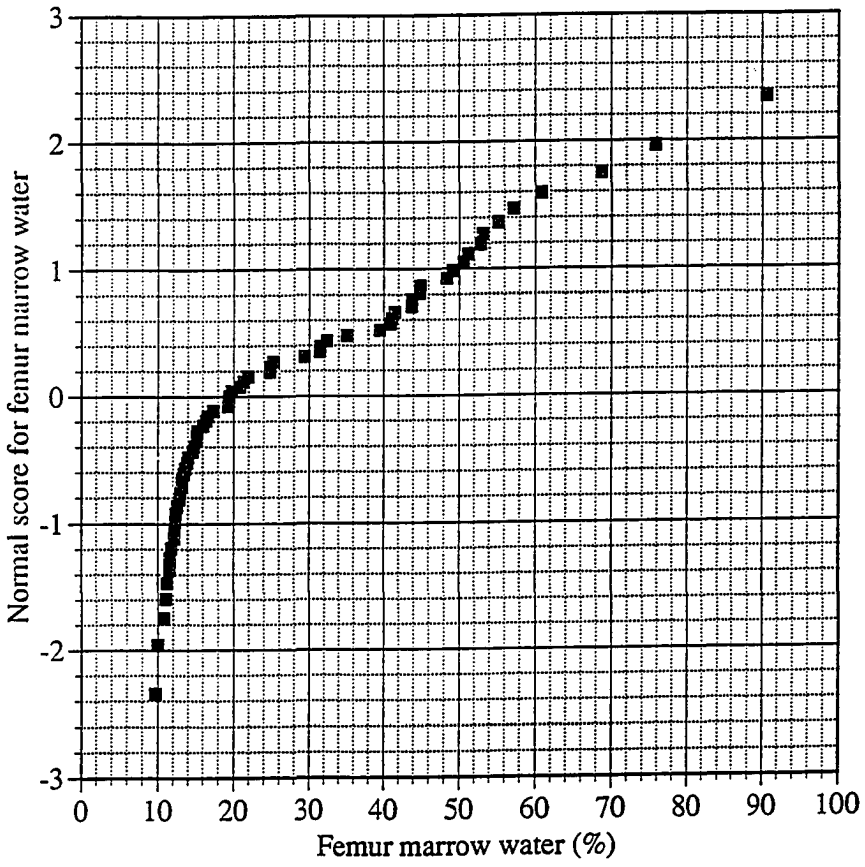

Figure 17. Relationship between femur marrow water (%) and its normal score.

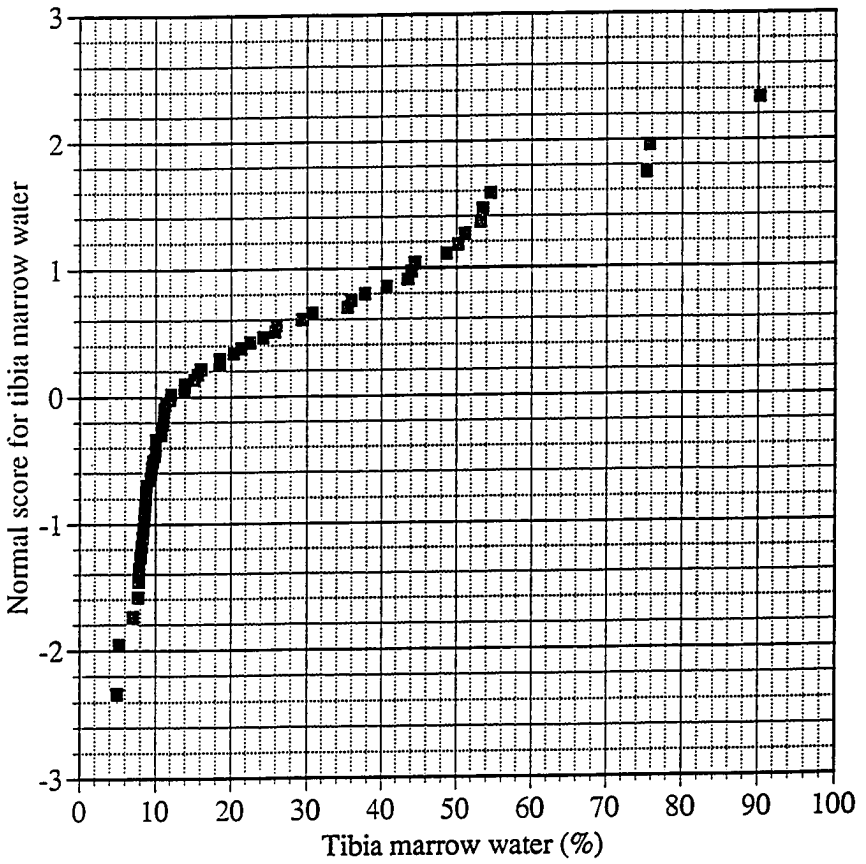

Figure 18. Relationship between tibia marrow water (%) and its normal score.

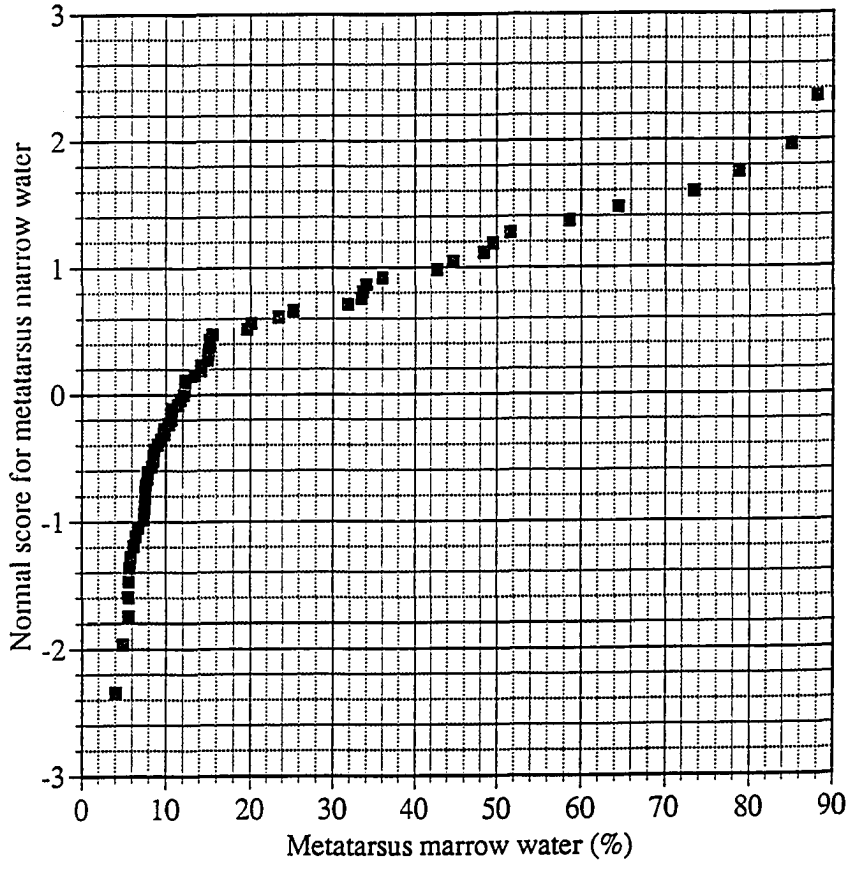

Figure 19. Relationship between metatarsus marrow water (%) and its normal score.

Table 14. Simple linear regressions for predicting carcass+viscera weight (y; kg) in female caribou aged > 24 months. See Figures 17-19 for normal scores (Nscore) of marrow water.

x	EQUATION	n	r^2	RMSE	p
CHEST	$y = -9.3 + 0.5461\,x$	64	0.19	6.5	0.0003
GASTR	$y = 14.6 + 0.0720\,x$	64	0.55	4.9	0.0001
GASH2O	$y = 275.7 - 2.9698\,x$	65	0.31	6.0	0.0001
PERTER	$y = 8.0 + 0.3183\,x$	65	0.62	4.4	0.0001
PERH2O	$y = 257.8 - 2.7036\,x$	65	0.30	6.0	0.0001
FEMWT	$y = 19.6 + 0.0961\,x$	64	0.19	6.5	0.0003
FMFWT	$y = 45.5 + 0.3447\,x$	64	0.32	6.0	0.0001
FMH2O	$y = 54.9 - 4.1249$ Nscore (x)	65	0.32	5.9	0.0001
TIBIAWT	$y = 20.6 + 0.1054\,x$	65	0.15	6.6	0.0013
TMFWT	$y = 42.7 + 0.3223\,x$	64	0.34	5.9	0.0001
TMH2O	$y = 54.9 - 3.9138$ Nscore (x)	64	0.29	6.1	0.0001
MMFWT	$y = 46.5 + 0.3310\,x$	65	0.18	6.5	0.0004
MMH2O	$y = 54.9 - 3.8115$ Nscore (x)	65	0.28	6.1	0.0001
BACKFAT	$y = 52.8 + 5.7537\,x$	65	0.43	5.5	0.0001
HEART	$y = 30.9 + 25.6406\,x$	61	0.42	5.5	0.0001
LIVER	$y = 37.7 + 14.3235\,x$	60	0.34	5.9	0.0001
RKIDFAT	$y = 46.0 + 0.3012\,x$	65	0.49	5.1	0.0001
RKFI	$y = 47.7 + 0.2381\,x$	65	0.32	6.0	0.0001
LKIDFAT	$y = 46.6 + 0.2645\,x$	65	0.56	4.8	0.0001
LKFI	$y = 48.3 + 0.2067\,x$	65	0.36	5.7	0.0001

There was a tendency for the four equations to err in the same direction within each collection period (Table 14). For instance, all equations underpredicted mean body weight in September 1989 and overpredicted in November 1989. However, this was not a seasonal effect because the underprediction of September 1989 was not duplicated in September 1990. Instead, variations in gut fill probably account for much of this effect, as animals collected in the same locale and timeframe probably experienced similar foraging opportunities.

There was also a tendency for the equations to underestimate at the heavy weight range and overestimate at the opposite weight extreme (Figure 20). This prediction bias was weak in Equations 1 and 2 but was more pronounced in Equations 3 and 4.

Carcass+Viscera Weight

The best single indices of body weight were also among the best single indices of carcass+viscera weight, with peroneus tertius weight and gastrocnemius weight again retaining the highest r-squares (Table 15). However, kidney fat and back fat also correlated strongly with carcass+viscera weight, and had higher r-squares than either heart weight or liver weight (Table 15).

All predictor variables, with the exception of percent marrow fat and percent marrow water, linearly correlated to carcass+viscera weight. Percent marrow fat correlated to carcass+viscera weight only when carcass+viscera weight was less than approximately 60 kg. Percent marrow fat saturated above this point and did not respond to further weight changes. Similarly, percent marrow water inversely

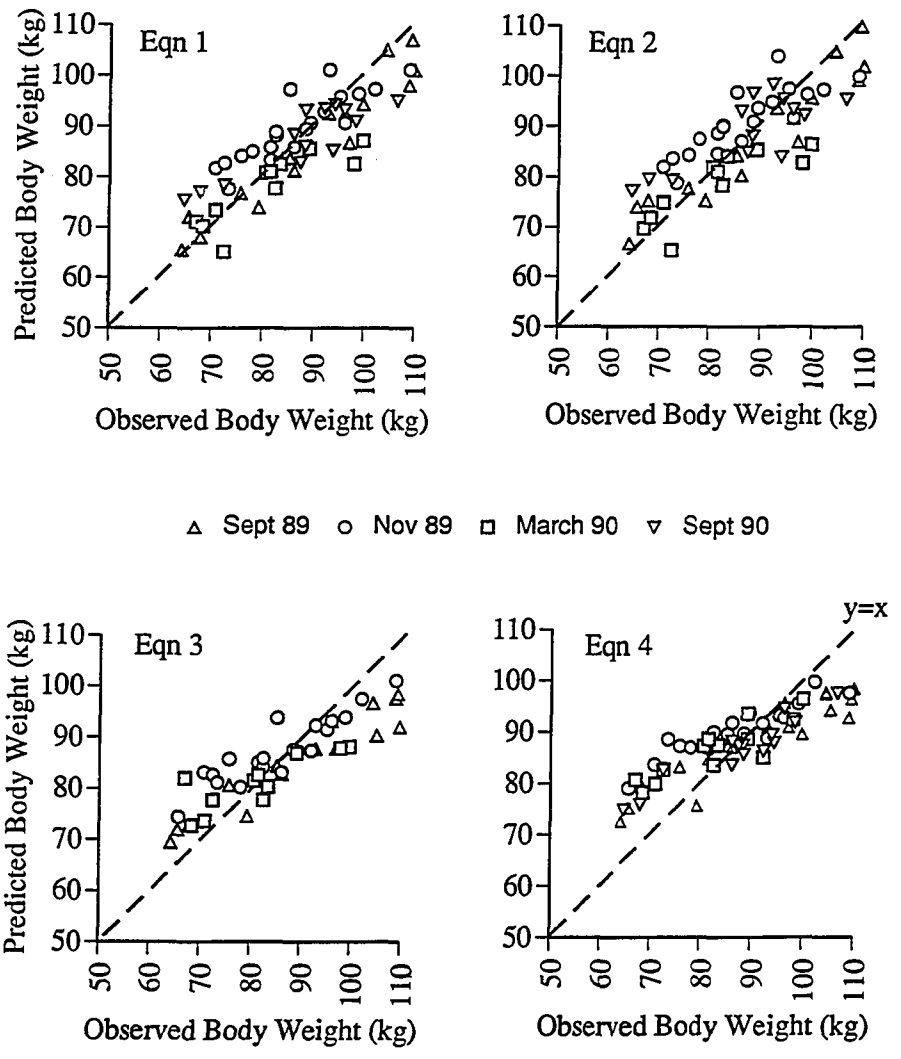

Figure 20. Comparison of actual and predicted body weights based on Equations 1 to 4 (Table 4).

Table 15. Simple linear regressions for predicting body fat (y; %) in female caribou aged > 24 months. See Figures 17-19 for normal scores (Nscore) for marrow water.

x	EQUATION	n	r^2	p
GASTR	$y = [\text{Sin}(0.1072+0.00035x)]^2 \cdot 100$	61	0.25	0.0001
GASLIP	$y = [\text{Sin}(0.1698+0.03425x)]^2 \cdot 100$	61	0.40	0.0001
GASH2O	$y = [\text{Sin}(2.5604-0.03035x)]^2 \cdot 100$	61	0.63	0.0001
PERTER	$y = [\text{Sin}(0.1083+0.00133x)]^2 \cdot 100$	61	0.21	0.0002
PERH2O	$y = [\text{Sin}(2.2416-0.02580x)]^2 \cdot 100$	61	0.51	0.0001
FMFWT	$y = [\text{Sin}(0.2058+0.00352x)]^2 \cdot 100$	60	0.61	0.0001
FMFH2O	$y = [\text{Sin}(0.3028-0.04474\ \text{Nscore}(x))]^2 \cdot 100$	61	0.65	0.0001
TMFWT	$y = [\text{Sin}(0.1963+0.00284x)]^2 \cdot 100$	61	0.53	0.0001
TMH2O	$y = [\text{Sin}(0.3050-0.04296\ \text{Nscore}(x))]^2 \cdot 100$	61	0.62	0.0001
MMFWT	$y = [\text{Sin}(0.2184+0.00328x)]^2 \cdot 100$	61	0.32	0.0001
MMH2O	$y = [\text{Sin}(0.3034-0.04406\ \text{Nscore}(x))]^2 \cdot 100$	61	0.60	0.0001
BACKFAT	$y = [\text{Sin}(0.2911+0.03970x)]^2 \cdot 100$	61	0.32	0.0001
RKIDFAT	$y = [\text{Sin}(0.2385+0.00222x)]^2 \cdot 100$	61	0.48	0.0001
RKFI	$y = [\text{Sin}(0.2333+0.00235x)]^2 \cdot 100$	61	0.53	0.0001
LIKDFAT	$y = [\text{Sin}(0.2370+0.00220x)]^2 \cdot 100$	61	0.58	0.0001
LKFI	$y = [\text{Sin}(0.2362+0.00220x)]^2 \cdot 100$	61	0.58	0.0001

correlated to carcass+viscera weight only when carcass+viscera weight was less than 60 kg.

The high r-square for peroneus tertius weight resulted in the inclusion of this variable in all multiple regressions of carcass+viscera weight (Tables 3 and 4). The exception was Equation 9, when peroneus tertius weight was intentionally excluded from the selection list to allow for situations where this muscle is unavailable. Equation 5 had the the highest predictability of carcass+viscera weight and consisted of 6 terms that included the normal score for femur marrow water (Table 12). Removal of femur measurements from the selection list yielded Equation 6, while removal of both femur and external measurements yielded equations 7 to 9. Reductions in r-squares associated with these increasingly constrained regressions did not exceed 0.03 until peroneus tertius weight was eliminated from the selection list in Equation 9.

Body Fat

The best predictors of body fat were all measurements of fat depots (Table 16). Of the 18 predictor variables that were not adipose measurements, only gastrocnemius weight (r^2=0.25), peroneus tertius weight (r^2=0.21), heart weight (r^2=0.09), and chest girth (r^2=0.08) significantly correlated with body fat percentage. These were not selected by stepwise regression when adipose measurements were present in the selection list.

Differential deposition and mobilization sequences of the various fat depots resulted in a significant seasonal effect in multiple regression prediction of body fat (Tables 3 and 4). Kidney fat and intramuscular fat in the gastrocnemius and peroneus

Table 16. Comparison of observed and predicted mean body weights (kg ± 2 standard errors) for four independent data collections using Equations 1 to 4 (Table 13).

	SEP 89	NOV 89	MAR 90	SEP 90
Equation 1				
n	16	20	11	13
Observed mean	89.0 ± 7.7	86.7 ± 4.6	81.3 ± 6.7	87.5 ± 6.8
Predicted mean	86.2 ± 6.5	89.7 ± 3.0	77.9 ± 2.1	87.1 ± 3.8
Difference	2.8	-3.0	3.4	0.4
Equation 2				
n	15	20	11	13
Observed mean	90.7 ± 7.6	86.7 ± 4.6	81.3 ± 6.7	87.5 ± 6.8
Predicted mean	89.0 ± 6.0	91.0 ± 3.0	78.3 ± 4.2	89.0 ± 4.1
Difference	1.7	-4.3	3.0	-1.5
Equation 3				
n	16	21	11	0
Observed mean	91.6 ± 7.3	85.7 ± 4.8	81.3 ± 6.7	
Predicted mean	86.5 ± 4.2	87.2 ± 2.7	81.0 ± 3.2	
Difference	5.1	-1.5	0.3	
Equation 4				
n	17	21	13	14
Observed mean	92.3 ± 7.0	85.7 ± 4.8	82.8 ± 6.0	87.4 ± 6.2
Predicted mean	89.2 ± 3.6	89.7 ± 2.1	86.4 ± 3.0	86.6 ± 3.3
Difference	3.1	-4.0	-3.6	0.9

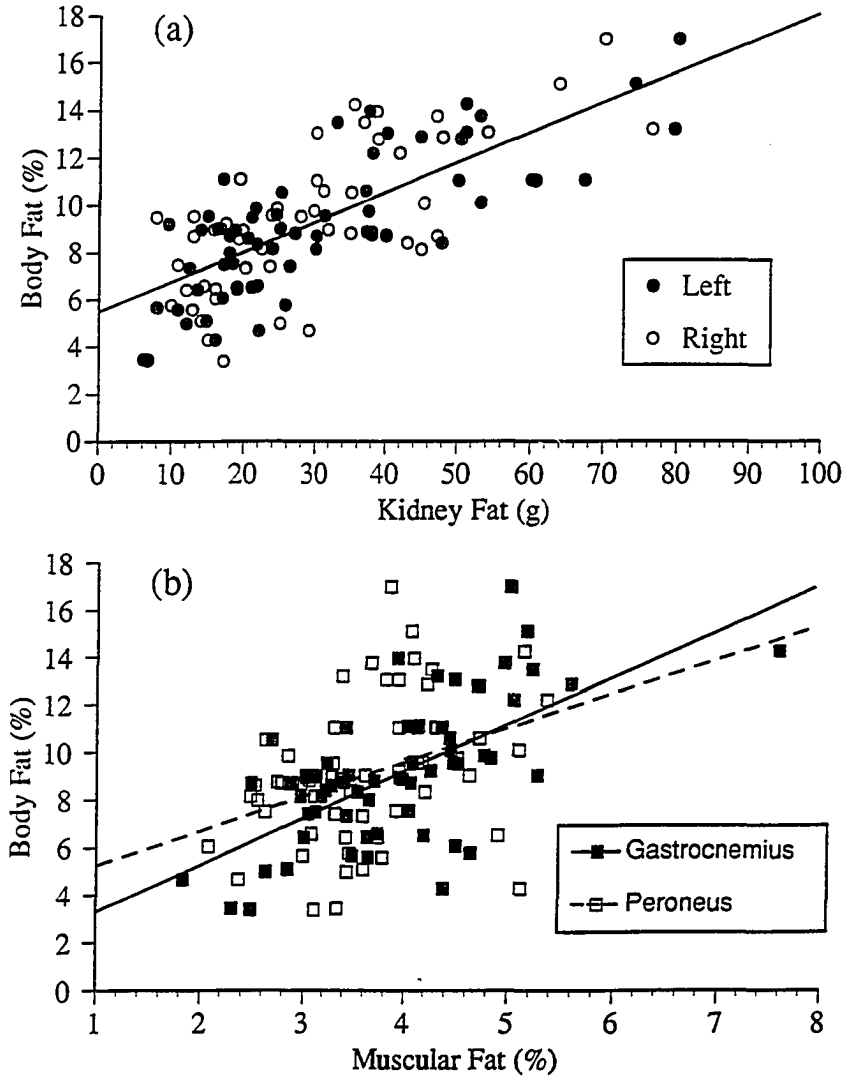

Figure 21. Relationships between percent body fat and (a) kidney fat weight (g) and (b) percent fat in indicator muscles.

tertius were linearly related to body fat (Figure 21), indicating constant changes in these indices over the entire range of observed body fat. However, percentage marrow fat in the femur, tibia-fibula, and metatarsus (Figure 22) approximated a saturation function similar to that for carcass+viscera weight. Marrow fat percentage became saturated at approximately 9% body fat for all 3 leg bones (Figure 22a), but a progressive increase in percentage marrow fat from femur to tibia-fibula to metatarsus (Table 17) suggests a depletion pattern advancing from the proximal to the distal bones. This pattern was particularly pronounced among seasonally lean animals in June and September. Marrow fat saturation coincided with a kidney fat weight of 15 to 25g (Figure 22b). Unlike marrow fat percentage, marrow fat weight in all leg bones retained a linear relationship with body fat (Figure 23).

Deposition of back fat was delayed until body fat approached 10% and percent marrow fat reached saturation (Figure 24). Back fat, when present, linearly correlated to body fat (Figure 24) only during the deposition phase between June and November. Among animals with no back fat, body fat distributions were seasonally clumped with values increasing progessively from lean, lipogenic animals in June to fat, lipolytic animals in March (Table 18). Thus, the early depletion of back fat in March preceded substantial fat mobilization elsewhere in the body.

The multiple regressions with the 2 highest r-squares required only 3 predictor variables in addition to season (Tables 3 and 4). Equations 10 and 11 have near-equivalent r-squares and differ only in their third predictor variable. Equations 12 and 13 have the simplified requirements of only 2 continuous predictor variables, and the weight of kidney fat from just the left kidney instead of both left and right kidneys. Equation 14, with the lowest r^2 at 0.73, does not require kidney fat weights.

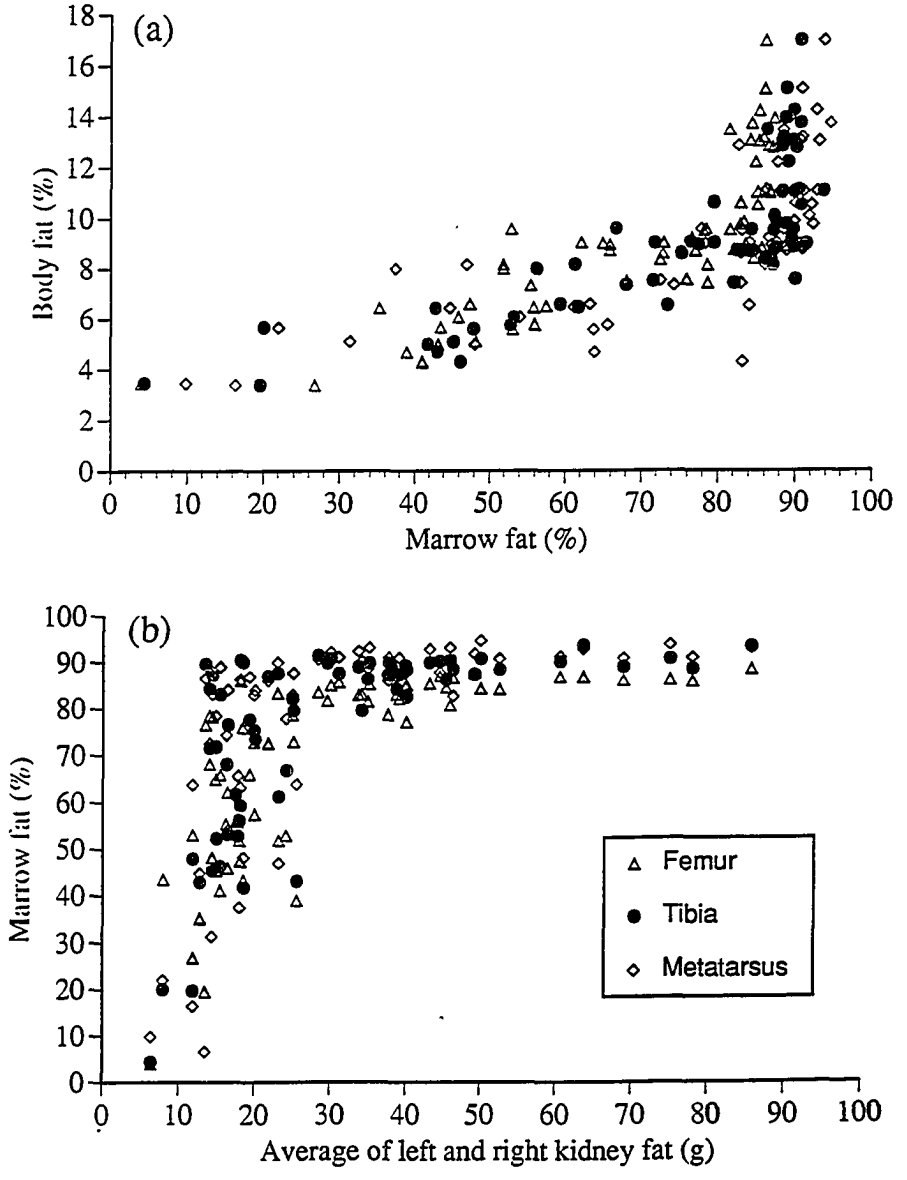

Figure 22. Relationships between percentage marrow fat and (a) percentage body fat; and (b) perirenal fat averaged for right and left kidneys.

Table 17. Difference (x-y) in percent marrow fat between long-leg bones. P-values shown for pairwise comparisons of arcsine transformed marrow fat percentages.

BONE x	BONE y	n	x-y	SE	p
June (6.4% mean body fat)					
Femur	Tibia	17	-2.5	0.8	0.005
Tibia	Metatarsus	17	-2.4	1.1	0.047
Femur	Metatarsus	17	-4.9	1.3	0.002
September (9.8% mean body fat)					
Femur	Tibia	11	-2.2	0.5	0.001
Tibia	Metatarsus	11	-1.8	0.7	0.049
Femur	Metatarsus	11	-4.0	0.9	0.001
November (9.9% mean body fat)					
Femur	Tibia	19	-2.1	0.4	0.000
Tibia	Metatarsus	19	-0.3	0.6	0.960
Femur	Metatarsus	20	-1.7	0.9	0.026
March (10.8% mean body fat)					
Femur	Tibia	17	-1.5	0.8	0.071
Tibia	Metatarsus	17	-0.7	0.5	0.160
Femur	Metatarsus	17	-2.2	1.0	0.035

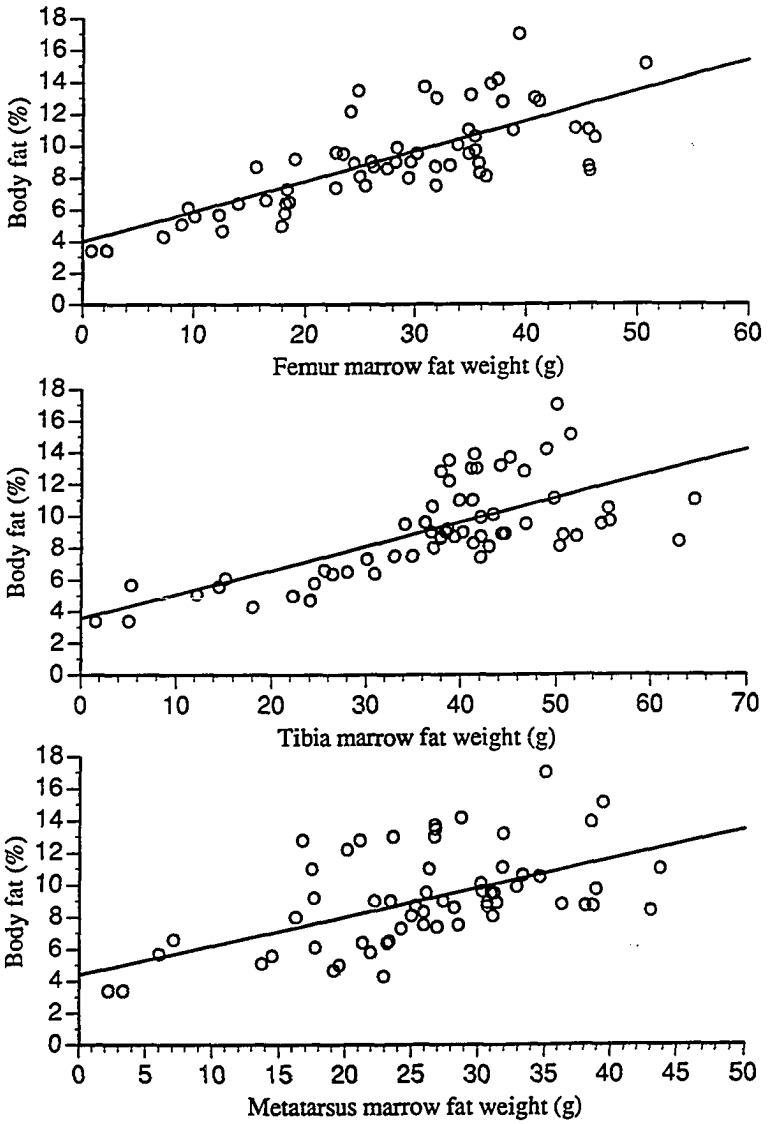

Figure 23. Relationships between body fat (%) and marrow fat weight (g) in the femur, tibia, and metatarsus.

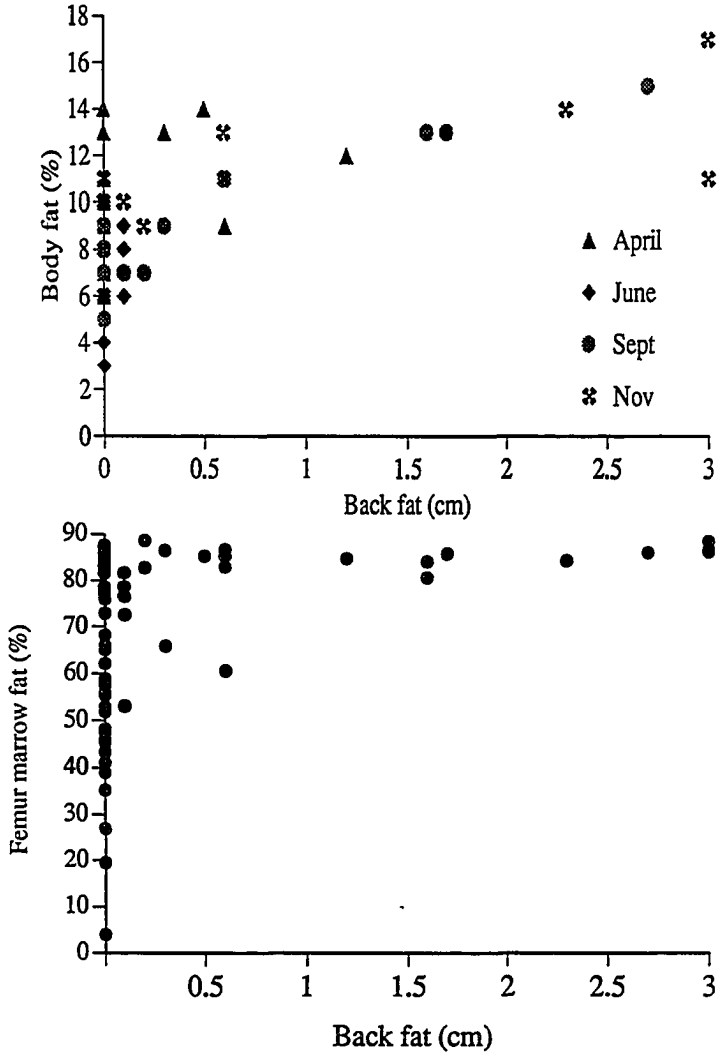

Figure 24. Back fat depth (cm) versus body fat (%) and femur marrow fat (%).

Table 18. Seasonal mean body fat (%) for female caribou with zero backfat. (Means with the same superscript are not significantly different at p=0.05).

SEASON	n	MEAN	MIN	MAX	SE
June	14	6.1[a]	3.4	9.6	0.5
Sept	4	7.5[ab]	4.7	9.0	1.0
Nov	11	8.6[bc]	6.4	10.5	0.3
March	13	10.2[c]	5.7	13.9	0.6

Body Protein

Metatarsus length (r^2=0.21), gastrocnemius fat (r^2=0.19), and heart weight (r^2=0.17) were the most important single indices of percent dry crude protein. The high partial correlation coefficients of metatarsus length and gastrocnemius fat repeatedly resulted in their selection into stepwise regressions (Tables 3 and 4). The exclusion of femur measurements from the selection list only reduced the adj-r^2 by 0.03 (Equation 16), but the concomittant exclusion of femur measurements, external dimensions, and gastrocnemius fat reduced the adj-r^2 by 0.21 (Equation 17).

The multiplier for converting body dry crude protein to body wet crude protein equalled 5.00 when data were pooled for all seasons (Table 19). However, significant seasonal differences revealed increasing values between fall and late winter (Table 19).

Table 19. Ratio of wet:dry crude protein weighted for smooth and skeletal muscle composition in female caribou. (Means with the same superscript are not significantly different at p=0.05).

SEASON	n	MEAN	MIN	MAX	SE
March	16	4.97[b]	4.62	5.30	0.048
June	17	5.37[a]	5.08	5.69	0.046
Sept	10	4.82[c]	4.66	4.98	0.031
Nov	18	4.79[c]	4.39	5.09	0.051
Pooled	61	5.00	4.39	5.69	0.039

Discussion and Management Implications

Body Weight

Body weight can be predicted with reasonable accuracy (Tables 3 and 4) but is confounded by large variations in gut fill, which ranged from 10.8 to 28.2% of body weight. Body weight in March-April is also confounded by the presence or absence of a gravid uterus, which weighed up to 8.6 kg (8.4 % of body weight). Nonetheless, reproductive status was not a significant predictor variable in stepwise regression, perhaps because concomitant variations in gut fill obscured the weight of the concepta. The biological interpretation of body weight is greatly complicated by such dual confounding, but the prediction of body weight remains necessary where comparison with live animals is desired.

The prediction bias denoted by overestimation at the low weight range and underestimation at the opposite weight extreme (Figure 20) may reflect the forced exclusion of variables that significantly affect body weight. The omission of an important independent variable is also a possibility with Equation (1) even though it was not artificially constrained during regression analysis. Additional predictor variables may not have gained significance because of inadequate sample size, or because of confounding by gut fill and pregnancy. The possibility of insufficient predictor variables is suggested by a progressive increase in prediction bias from Equations 1 to 4 (Figure 20) that accompanied the progressive decline in number of predictor variables. The observed prediction bias also suggests a weakened relationship between predicted and predictor variables at extreme body weights. However, this is not supported by the lack of curvilinearity in the simple regressions

between body weight and individual indices. A linear relationship between indicator muscle and carcass weight is also supported by data from Ringberg et al. (1981) on reindeer. The observed prediction bias is especially perplexing because it was not apparent in the regression residuals of the original data set for Equations 1 to 3. Regression residuals for Equation 4 did show a slight pattern of underprediction among heavy animals.

The prediction bias, if genuine, is not neccessarily unacceptable for body weight monitoring at the population level because it will not affect results for interannual trends. In fact, Equation 4 produced less variance between observed and predicted values than the other 3 equations (Figure 20) despite its pronounced bias. Given the serious confounding effects of gut fill and pregnancy, body weight can never be predicted with absolute precision and therefore may not warrant prodigious attempts to do so. Nonetheless, the recognition of potential biases in Equations 1 to 4 is important because prediction accuracy will depend heavily on an adequate random sample that precludes over-representation at either weight extreme. In this study, the consistent prediction by all equations within the 95% confidence interval of the observed mean supports the legitimacy of sample sizes between 11 and 24 that were used during validation. Recognition of potential equation biases is also important because the slope of less than unity characterizing predicted and actual body weights (Figure 20) effectively downscales the body weight unit. Consequently, significant changes in mean body weight should be correspondingly inflated to reflect true changes in mean body weight.

An equation bias can be easily rectified by the application of a corrective slope based on Figure 20. However, this procedure is not recommended without further validation because a prediction bias is not supported by the regression residuals of the

original data set. Additionally, the possibility of observer bias cannot be precluded. The independent data collections were collaboratively conducted by multiple personnel and this increases the probability for both measurement error and observer bias. Such bias is especially prone when rectilinear scales are used for body weight measurements because of the susceptibility to parallax. Thus, the independent data collections are equally a test of managerial implementation of a monitoring program as well as one of equation validation.

Carcass+Viscera Weight

Carcass+viscera weight can be predicted with much higher precision than body weight because it is not confounded by either pregnancy or gut fill. The regression equation with the highest adj-r^2 required 6 measurements that included an external dimension, 3 organ weights, and 2 adipose indices. Of these, only femur marrow water required minimal lab work in the form of freeze-drying. Back fat was an important adipose index in heavy animals. Left kidney fat was consistently selected over right kidney fat, perhaps because the longer mesenteric attachment provided the opportunity for greater fat accummulation. The high partial correlation coefficient for peroneus tertius weight is favorable for body condition monitoring because it is an easily obtained variable requiring minimal labor.

Body Fat

The late deposition and early mobilization of back fat reported in this study concur with earlier research on cattle (Berg and Butterfield 1976) and caribou

(Dauphiné 1971, Adamczewski et al. 1987). However, the phase-dependent relationship between body fat and back fat has not been previously reported, and is an important consideration in the use of this condition index. Back fat is easily measured and accessible, and especially propitious because it can be calibrated in live animals by either ultrasound or biopsy. However, the lack of relationship between back fat and percent body fat during weight loss restricts the use of this adipose index to periods of positive energy balance between June and September (Chapter 1). A decoupling of the relationship between back fat and percent body fat during weight loss, but a phase-independent correlation between back fat and carcass+viscera weight, suggest significant protein catabolism concurrent with subcutaneous fat mobilization. This observation is supported by data on mule deer (Torbit et al. 1985) indicating the importance of protein catabolism during the initial stages of negative energy balance, even among animals experiencing only a slight energy deficit. The retarded deposition of back fat has been explained (Berg and Butterfield 1976) on the basis of local tissue resistance, with fat accumulation initially occurring at low pressure sites between and around muscles and organs. A more physiological explanation advanced by Frish (1984) suggests a higher priority for periorganal fat depots to permit localized increases in metabolic rate.

The delayed deposition of subcutaneous fat contrasts with the early deposition and late mobilization of bone marrow fat. The higher marrow fat contents in the proximal than the distal bones agree with earlier data for moose (Peterson et al. 1982), caribou (Davis et al. 1987), and white-tailed deer (Fuller et al. 1986), and may reflect a depletion sequence advancing from the proximal to the distal extremities. This interpretation is supported by current observations indicating that differences between the femur and metatarsus marrows are particularly exaggerated in seasonally lean

animals in June (Table 17). However, maximum fat content is also lower for proximal than distal bone marrows (Figure 22a), and observed differences may therefore be attributable to lower initial values in the femur. Differential marrow composition between sites has previously been shown by Meng et al. (1969), who documented a progressive increase in the double-bonding of marrow fat from the proximal to the distal leg bones in caribou.

This study demonstrated that marrow fat weight does not follow the saturation function characterizing percent marrow fat, but linearly correlates with percent body fat throughout the entire range of observed values (Figure 23). Thus, contrary to widespread perception (Dauphiné 1971, Mech and DelGiudice 1985, Fuller et al. 1986, Adamczewski et al. 1987, Torbit et al. 1988), marrow fat can be a useful index of both fat and lean animals when it is broadened to include marrow weight, and is not limited to percent marrow fat as is conventionally the case (Dauphiné 1971, Anderson et al. 1972, Huot and Goudreault 1985, Nieminen and Laitinen 1986, Adamczewski 1987). The measurement of marrow fat weight is slightly more cumbersome because it requires the complete extraction of bone marrow in addition to the determination of marrow fat percent. However, its linearity with percent body fat simplifies the multiple regression procedure by eliminating the transformation required for a saturation function. This advantage notwithstanding, percent marrow fat was frequently selected over marrow fat weight in multiple regression analysis, perhaps because the early dynamics of the former better complements, and not just parallels, other adipose indices.

With the exception of back fat and marrow fat, all other adipose indices were linearly correlated with percent body fat. The linearity of intramuscular fat concurs with work by Ringberg et al. (1981) and Huot and Goudreault (1985). However, Huot

and Goudreault (1986) found a distinctly curvilinear relationship between kidney fat index and body fat percentage, while Finger et al. (1981) and Torbit et al. (1988) considered both linear and log transformed models to be appropriate.

The kidney fat index has been criticized as a poor indicator of body condition because kidney weight fluctuates seasonally (Dauphiné 1975, Van Vuren and Coblentz 1985). Nonetheless, highly significant relationships between kidney fat index and percent body fat were found in this and other studies (Finger et al. 1981, Huot and Goudreault 1985, Torbit et al. 1988). The kidney fat index can be a good predictor of body fat despite seasonal fluctuations in kidney weight because it reflects seasonal ratios of fat to lean. However, the kidney fat index does not have any predictive advantage over kidney fat weight, and has the disadvantage of an additional weight measure. In multiple regression analysis, kidney fat weight was invariably selected over the kidney fat index when both were included in the independent variable list.

Because adipose indices are a direct consequence of body fatness, body fat percent can be predicted with high precision and with fewer parameters than body weight, carcass+viscera weight, or body protein.

Body Protein

Dry crude protein is difficult to predict because it is a relatively constant proportion of fat-extracted dry tissue, averaging 72.0% of fat-free dry matter regardless of season. Much of the variability in this proportion is attributable to random variation, and consequently, predictive ability is severely limited. Additionally, the prediction of dry crude protein, as a proportion of wet tissue, must

also account for the proportions of fat and water in wet tissue, as well as the proportion of crude protein in fat-free dry matter. Thus, the predictability of dry crude protein is lower than for the other 3 dependent variables, despite the use of 5 predictor variables in the best regression equation (15).

Crude protein is conventionally reported on a dry weight basis in body composition studies (Reimers et al. 1982, Huot 1989). However, the conversion of dry crude protein to wet crude protein, as a proportion of wet tissue, permits the assessment of relative changes in adipose and lean tissue for a given change in body weight. Comparison with data for dissectable muscle is also facilitated.

Implementation of Monitoring Program

The selection of equations to be used in a monitoring program will depend on both management objectives and resources, as well as specific characteristics of the population in question. Where the sole objective is to monitor population trend, the use of suboptimal equations is probably adequate for detecting relative changes over time, especially if economic and logistical constraints are limiting. Equations with lower r-squares sacrifice on precision but fewer predictor variables may allow the trade-off to a larger sample size. Conversely, such equations may inadequately account for variation over the entire range of the independent variable, thereby increasing the likelihood of bias at extreme values. Additionally, absolute predicted values are particularly compromised on single or small sample sizes.

The best predictive equations for body weight, carcass+viscera weight, body fat, and body protein collectively require 14 measurements. Of these, 11 can be measured directly in the field, while the remaining 3 require labwork. Labwork is

non-technical in the drying of femur and tibia-fibula marrow, but entails specialized equipment for fat extraction of the gastrocnemius muscle. Gastrocnemius fat content, while not required for prediction of either body or carcass+viscera weight, was essential for maximum predictability of body fat and body protein. Unfortunately, neither gastrocnemius water content, which is inversely related to gastrocnemius fat content and more easily measured, nor fat content of the peroneus tertius, a smaller muscle more willingly surrendered by hunters, were satisfactory replacements.

Because of equation overlap, reducing the number of variables to be predicted does not proportionately reduce the number of predictor variables. The best predictive equations for carcass+viscera weight and body fat, ostensively the two most important condition parameters, require 9 measurements, in contrast to the 14 required for the prediction of all four independent variables. The best equations for body weight, carcass+viscera weight, and body fat collectively require 13 predictor variables. Thus, the additional prediction of body protein requires only 1 more measurement than those already needed for the other 3 parameters.

The minimum number of predictor variables needed to predict all four condition parameters is 8, with Equations 3 and 9 sharing 3 indices for projecting body and carcass+viscera weights respectively. The remaining 5 indices consist of kidney weight and 4 metatarsus measurements for predicting body fat and body protein (Equations 13 and 18). The number of indices increase to 13 when the only constraint is to exclude femur measurements and not to minimize predictor variables (Equations 2, 6, 10, 16).

In addition to equation selection, implementation of a monitoring program requires additional considerations such as sample time and sample cohort. The decision on what time of year to sample depends as much on monitoring objectives as

sample protocol, since the same predictive equations can be used throughout the year. September is probably the preferred time to sample if the objective is to monitor potential changes in summer habitat, project pregnancy rate in October, or assess readiness for winter survival. Alternatively, June is the preferred choice if the objective is to monitor potential changes in winter habitat, or to assess the potential for lactation before green-up. Although body weight and composition ultimately depends on both winter and summer conditions, carry-over effects from the preceeding season will generally be eclipsed by current environmental conditions. In some situations, multiple samples per year may be neccessary to address different monitoring objectives.

Superimposed on the above objectives is the added consideration of whether the results should reflect interannual variation due to climatic effects, or variations due to long term habitat changes. If the latter is true, then late November may be the least desirable time to sample since body composition changes extremely rapidly in weaning females and collection of repeatable data becomes limited to a very narrow time window. Alternatively, early weaning may reflect good summer conditions, and consequently, late November would be a good sampling time if the objective is to monitor interannual variations. Sampling in late November also permits determination of conception rate. Among breeding females, body weight, body fat, and body protein reserves all reach annual minima shortly after calving in June (Chapter 1). Additionally, the convergent effects of winter result in more stable body condition values at this time of year (Chapter 1). Consequently, significant condition shifts in June may well reflect habitat changes rather than weather patterns.

This study focused on mature females, but monitoring objectives may choose to emphasize another cohort. The extrapolation of predictive equations to male

caribou should be done with extreme caution since physiological and anatomical differences may result in sex-specific composition indices. However, limited data for males showed consistency with the female-generated regressions between body weight and gastrocnemius weight, and between percent body fat and 2 adipose indices, kidney fat weight and percent femur marrow fat (Figure 25). Similarly, immature female caribou aged 4-22 months did not obviously deviate from regressions generated by data on mature females (Figure 25).

Regression slopes and intercepts relating body weight to gastrocnemius weight differed significantly between adult females and calves aged 1-3 months (Figure 25). The calf regression, which passed through the origin and had a higher slope than that for the adult females, is consistent with an undeveloped rumen and low gut fill. Relationships between body fat and adipose indices are lacking for calves but may also differ from those of adults. In mule deer, both the kidney fat index and percent femur marrow fat were significantly lower in fawns than in adult females for a given body fat composition (Torbit et al. 1988). Caribou calves from Coats Island did not differ from adult females in regressions between gastrocnemius weight and dissectible carcass muscle weight, nor between femur weight and dissectible carcass bone weight (Adamczewski et al. 1987). However, dissectible muscle weight includes both protein and fat reserves, and the relative composition of these two are expected to change with age (Berg and Butterfield 1976).

The use of bone, muscle, organ, and fat indices to predict body weight and composition is a viable technique for monitoring population condition in caribou. Indices can be used either singly or in combination depending on data availability and required levels of precision. Body weight, which is confounded by ingesta content and the presence or absence of a fetus, is more difficult to predict than combined

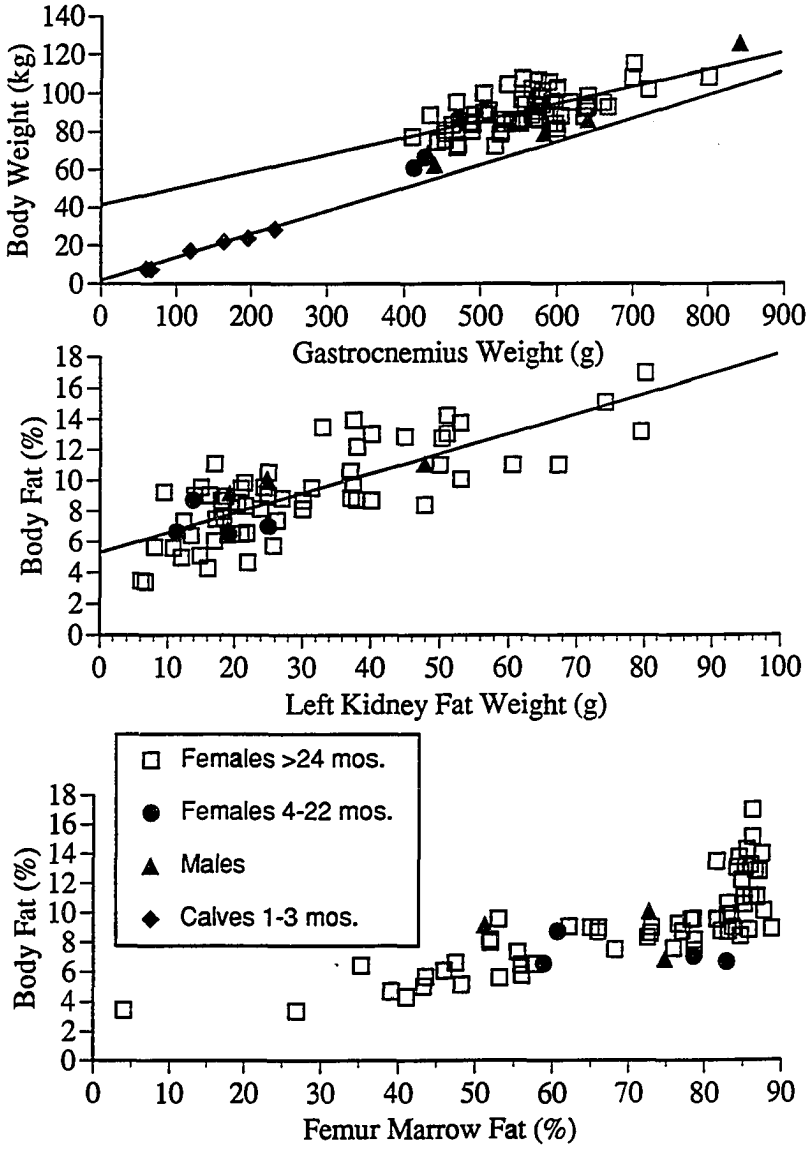

Figure 25. Comparison of body weight and body fat indices in mature females (>24 months), immature females (4-22 months), males, and calves less than 3 months old.

carcass and viscera weight, which provide a better measure of body reserves. Adipose indices directly reflect total fat reserves and yielded highly repeatable predictions even when used individually.

Synopsis

Nutrient partitioning allocates limited substrates between competing body tissues and is especially consequential in caribou and reindeer because realized body composition affects virtually every aspect of reproduction and survival (Klein 1968, Dauphiné 1976, Thomas et al. 1976, Haukioja and Salovaara 1978, White 1983, Reimers et al. 1982, Reimers 1983a, 1983b, Rognmo et al. 1983, Leader-Williams and Rosser 1983, Skogland 1983, 1984, Cameron et al. 1991). In breeding females, nutrient partitioning must also allocate substrates between dam and offspring under asynchronous changes in food resources and reproductive expenditures. Nutrient partitioning strategies and the factors regulating such strategies are therefore vital to the fitness of caribou and reindeer, and is pivotal to the understanding of this species.

In this study, I found that reproductive status was a predominant factor in the trade-off between body fat and body protein deposition. Among free-ranging caribou, both breeding and non-breeding females experienced maximal tissue gain between June and September, but the preferential deposition of body protein by lactating females contrasted sharply with the preferential deposition of body fat by non-lactating females. As a result, lactating females were seriously compromised in their ability to replenish fat reserves during the summer, and accumulated only 20% as much body fat as non-lactating individuals. In contrast, body protein deposition was largely unaffected by lactation and was nearly comparable between the two reproductive cohorts.

The priority for protein deposition among breeding females in the wild were also observed in pen-fed animals in captivity. Whereas non-lactating females

increased fat deposition with increased energy intake, lactating females increased protein deposition. Additionally, the proclivity of lactating females to sacrifice body fat for milk production contrasted with their relative disinclination for doing the same with body protein.

The leading priority for body protein deposition in lactating females reveals the limit to which maternal requirements will be compromised for current recruitment. In this study, milk fat and energy output were independent of either maternal fat reserves or maternai nutrition, and this indicates a seemingly open-ended commitment to supplying milk energy between 60 and 100 days post-partum. In contrast, the significant correlation between milk protein output and the maternal dietary protein:energy ratio suggest a more conservative use of maternal body protein. Protein conservation is propitious given the multiple non-discretionary functions of amino acids and proteinaceous tissue, and is underscored by the seasonal stability of total body protein in both free-ranging and captive animals. Additionally, protein repletion over the summer is especially critical given the lack of subsequent opportunities over the prolonged winter.

A conservative use of body protein is also critical to future reproductive success, not only as mediated through maternal welfare, but also through fetal growth and birth weight. In this study, fetal weight in March-April and birth weight in June both correlated significantly with only maternal body protein, and not maternal body fat. These results further underscore the unique and distinct role of protein beyond that of energy source.

A conservative production of milk lactose was also apparent in lactating caribou and reindeer. In contrast to production of all other milk parameters, milk lactose production declined significantly with calf age and increased significantly with

increased maternal energy intake. A conservative milk lactose output has been proposed to spare glucose carbon for maternal functions (White and Luick 1984). At the same time, the concentrated milk resulting from low lactose concentrations minimizes nursing time and hence, the potential for predation.

The trade-off between body fat and protein deposition was found to be seasonally dependent. In summer, body compositions diverged between the two breeding cohorts as non-lactating females realized rapid adipose gain. Following September, body compositions converged in the two cohorts as non-lactating females endured rapid lipolysis. The divergent effects of summer, and the convergent effects of winter, were clearly reflected in inter-cohort differences that were most pronounced in November and least pronounced in June. In both breeding and non-breeding females, fat deposition increased relative to protein deposition between spring and fall.

Knowledge of nutrient partitioning can be used in the diagnostics and monitoring of population body condition. Body weight and body composition of caribou can be predicted with reasonable to good accuracy using indices of bones, muscles, fat, and organs from hunter-killed animals. However, sequential deposition of different fat depots must be taken into consideration especially in the case of back fat, which linearly correlates to body fat during weight gain but is disassociated from body fat during weight loss. Early saturation of percent marrow fat in the femur, tibia-fibula, and metatarsus prompted earlier criticism of this index in fat animals (Dauphiné 1971, Mech and DelGiudice 1985, Fuller et al. 1986, Torbit et al. 1988). However, I demonstrated that marrow fat can be a useful index in both fat and lean animals when it is expressed as marrow fat weight, or when percent marrow fat is transformed with the normal score.

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